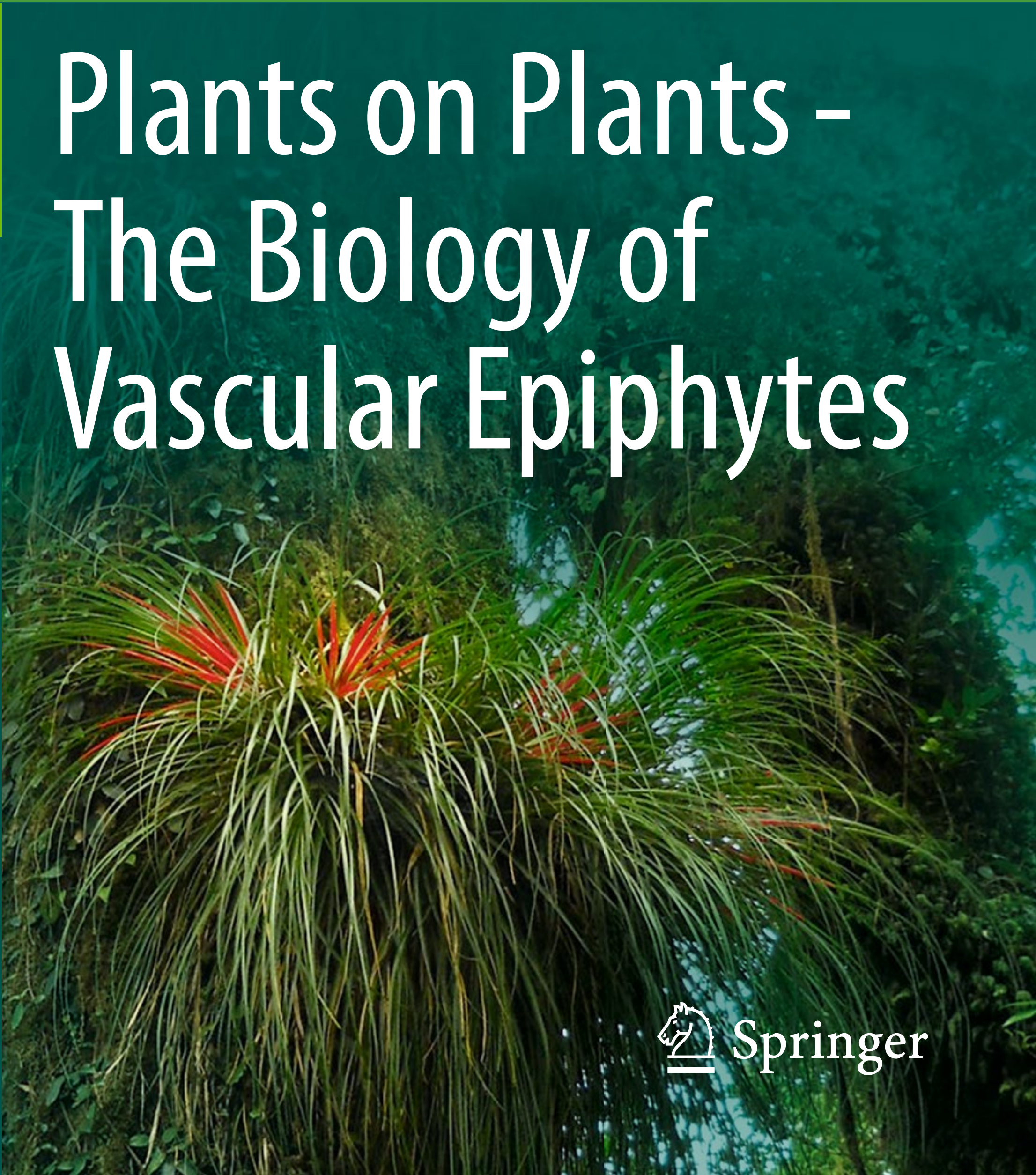
Fascinating Life Sciences

Gerhard Zotz

Plants on Plants - The Biology of Vascular Epiphytes



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Plants on Plants – The Biology of Vascular Epiphytes

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Cover illustration: Cover photo shows epiphytic *Fascicularia bicolor* in a temperate rainforest near Huinay (Chile), courtesy of Simon Pfanzelt

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Preface

Epibiota, organisms which live on other living things, are a fascinating facet of life on earth. A barnacle on a blue whale, a tiny diatom on a huge kelp, a liverwort on a palm leaf in the understory of a rainforest, and a huge tank bromeliad in the outer crown of a giant tree have quite a few things in common, but there are also a large number of distinctions. My initial plan was to write a book with a very broad taxonomic scope, covering at least the phenomenon of epiphytism in terrestrial, i.e., non-marine and non-limnetic, systems. This would have resulted in the treatise of epiphytic vascular plants, lichens, mosses, liverworts, and (terrestrial) algae such as *Trentepohlia* sp. It took a few months for me to realize that covering the biology of vascular epiphytes in the desired depth would already be enough of a challenge for a single person. Hence, I narrowed the scope to the biology of the approximately 28,000 species of vascular plants which always or primarily occur on other plants. The reader will see that this does not mean, however, that I am ignoring nonvascular epiphytes or other canopy-living organisms.

As much as possible, I tried to identify open research questions and to connect the particular case of vascular epiphytes to general biological principles, hoping that this will make stimulating reading both for the advanced graduate student, who is, e.g., looking for an interesting project, and for the senior scientist turning to epiphytes because there may be a connection with the organisms he or she is studying. The final product of my efforts may also be seen as the successor of a book that has been the reference for those with a genuine interest in vascular epiphytes for more than a quarter century, David H. Benzing's seminal "Vascular epiphytes," which was published in 1990. I can only hope that my book will be as stimulating and useful a resource as David's book has been for me and many others for the last decades. Initially planning to write in "dry" scientific prose, I soon decided to include personal comments on desirable directions and to be rather explicit in pointing out particular areas that I consider understudied. A provocative statement here and there is arguably a way to stimulate interesting science. If you disagree about a particular point of view, let me know—and let's start a discussion about the best way to move forward.

Oldenburg, Germany
February 2016

Gerhard Zotz

Acknowledgments

Science is a social endeavor. Hence, this single-author monograph is not the isolated achievement of one person but builds on the work of many others. I have tried to acknowledge this contribution of others with numerous citations, which in the end yielded a substantial citation list. However, it is simply impossible to cite all papers that contributed in one way or the other to this book in a comprehensive way. My personal collection of publications that contain information on vascular epiphytes sums up to almost 7000 papers, books, book chapters, theses, or reports. I apologize if your paper is not cited—I had to make a choice. This does not suggest any underlying judgment of quality or importance.

In addition, I had countless conversations with colleagues and students on my favorite subject over the last two decades, which helped to form the ideas and conclusions of this book. I also use unpublished information. For example, Cat Cardelús (Colgate, USA), Michael Kessler (ETH, Switzerland), and Nico Blüthgen (Darmstadt, Germany) provided extensive datasets on nutrient concentrations. Wolfgang Wanek (Vienna, Austria) shared unpublished data on nutrient uptake and Peter Hietz (Vienna, Austria) unpublished biomass data. Finally, I thank Rhett Harrison (Kunming, PR China) for sharing insights into the biology of hemiepiphytes.

A number of colleagues (Dirk Albach, Jose-Luis Andrade, Catherine Cardelús, Helena Einzmann, Peter Hietz, Michael Kessler, Holger Kreft, Thorsten Krömer, Glenda Mendieta Leiva, Heidi Meudt, Ana Silvia Moreira, Simon Pfanzelt, Alfredo Saldaña, Katrin Wagner, and Wolfgang Wanek) read drafts of individual chapters and I am grateful for their suggestions and frank criticism. Others helped out with specific information on canopy anurans, euglossine bees, or C4 photosynthesis (Shawn McCracken, David Roubik, and Rowan Sage). Having said this, I am solely responsible for any factual mistakes or interpretations you may disagree with. I am happy to take any criticism.

I thank Herta Sauerbrey (University Oldenburg) and Angel Aguirre (Smithsonian Tropical Research Institute—STRI) for all the help in procuring literature over many years. Dirk Albach, Peter Bak, Wilhelm Barthlott, Kevin Burns, Damian Catchpole, Gerhard Gottsberger, Michael Kessler, Moritz Klinghardt, Bejat McCracken, Ana Silvia Moreira, Steve Pearce, Rick Riefner, David Roubik, Steven Sylvester, and Christian Ziegler generously offered photographs. Laura Kuijpers, Christian König, and Holger Kreft helped with the geographical data and the preparation of the global distribution figures. Katrin Wagner supplied modified versions of graphs of previous publications. Vera Mageney and Dirk Albach helped with the figure on the relationship of pseudobulbs, epiphytism, and phylogeny in the Epidendroideae. Joachim Beyschlag provided a graph illustrating the potential of Y-Plant.

Last but not least, I also want to acknowledge the financial support by a number of institutions that made it possible for me to work on the biology of epiphytes for so many years, most prominently the DFG, but also the DAAD, STRI in Panama, the Jubiläumsstiftung in Würzburg, Germany, and the Freiwillige Akademische Gesellschaft in Basel, Switzerland.

A Comment on Plant Names

Accepted species names are not constant but rather frequently change with taxonomic revisions. For consistency, I only use names that are *currently* accepted in the online database “The Plant List” (accessed December 2015), even when other names were used in the original publications. The following list compares the currently accepted names with those in the original publications.

Name used in original publication	Currently valid name	Family
Didymopanax pittieri	*Schefflera rodriguesiana*	Araliaceae
Epidendrum macrostachyum	*Beclardia macrostachya*	Orchidaceae
Ficus stupenda	*Ficus crassiramea* subsp. *stupenda*	Moraceae
Guzmania minor	*Guzmania lingulata*	Bromeliaceae
Laelia cinnabarina	*Cattleya cinnabarina*	Orchidaceae
Lecanopteris sinuosa	*Myrmecophila sinuosa*	Polypodiaceae
Oncidium enderianum	*Oncidium praetextum*	Orchidaceae
Pitcairnia flavescens	*Pitcairnia albiflos*	Bromeliaceae
Pleopeltis polypoidoides	*Polypodium polypodioides*	Polypodiaceae
Polypodium phvllitidis	*Campyloneurum phyllitidis*	Polypodiaceae
Polypodium crassifolium	*Niphidium crassifolium*	Polypodiaceae
Psygmorchis pusilla	*Erycina pusilla*	Orchidaceae
Psygmorchis glossomystax	*Erycina glossomystax*	Orchidaceae
Rhipsalis heteroclada	*Rhipsalis teres*	Cactaceae

List of Abbreviations

Abbreviation	Full term	Comments
A	Net CO_2 uptake	
ABA	Abscisic acid	A plant hormone
$A_{\max}$	Maximum rate of net CO_2 uptake	In contrast to photosynthetic capacity (PC), $A_{\max}$ is determined at ambient CO_2
a.s.l.	Above sea level	
ATP	Adenosine triphosphate	Coenzyme involved in intracellular energy transfer
RWC	Relative water content	(FW – DW)/(maximum FW – DW)
CAM	Crassulacean acid metabolism	Photosynthetic pathway with nocturnal CO_2 uptake (see glossary)
^{13}C	Carbon-13	A natural isotope of carbon
$\delta^{13}C$		Measure of the relative abundance of the heavy isotope ^{13}C in a sample
dbh	Diameter at breast height	Standardized way of measuring trunk diameter
DOM	Dead organic material	
DW	Dry weight in g	
EQ	Epiphyte quotient	→Glossary
EFN	Extra-floral nectaries	
FW	Fresh weight in g	
g_w	Stomatal conductance for water vapor	Based on Ohm's Law. Calculated from the measured transpiration rate and the estimated gradient of water vapor between leaf and atmosphere (unit: mmol m^{-2} s^{-1})
IUCN	International Union for Conservation of Nature and Natural Resources	An international nongovernmental organization dedicated to the gathering and analysis of data, education, and lobbying. Publishes, e.g., the IUCN Red List of threatened species
LAR	Leaf area ratio	The amount of leaf area per unit total plant mass (see growth analysis)
LMR	Leaf mass ratio	Proportion of leaf biomass to total biomass

(continued)

Abbreviation	Full term	Comments
MAP	Mean annual precipitation	Average of several annual rainfall integrals
MAT	Mean annual temperature	Average of several annual averages of air temperature
MYA	Million years	
^{15}N	Nitrogen-15	A stable isotope of nitrogen, frequently used in ecological studies to trace fluxes
$\delta^{15}N$		Measure of the relative abundance of the heavy isotope ^{15}N in a sample
NAR	Net assimilation rate	The increase in plant mass per unit leaf area and time (see growth analysis)
NPP	Net primary production	→Glossary
PC	Maximum rate of net CO_2 uptake	In contrast to A_{max}, PC is determined at saturating CO_2
PFD	Photon flux density	Solar radiation in the range of 400–700 nm
PWC	Plant water content	Water stored in plant tissue in g plant^{-1}
RGR	Relative growth rate	Biomass increment per unit of initial biomass in a given time interval, usually expressed as g g^{-1} day^{-1} or day^{-1} (see growth analysis)
s.l.	Sensu lato	
SLA	Specific leaf area	Usually defined as the single surface area divided by dry mass

Contents

Introduction

1

1.1 What Is an Epiphyte?

Two hundred years ago, Mirbel (1815) was the first to define epiphytes as “plants that germinate on other plants without taking their nourishment from them” (in the original French version: “qui naissent sur d’autre végétaux, mais n’en tirent point leur nourriture”). The definition used in this treatise is very similar. Epiphytes are “plants that germinate and root non-parasitically on other plants at all stages of life.” In the real world, the application of this definition faces problems, since epiphytism grades into the soil-rooted habit. Quite a few epiphytic species grow occasionally on rocks or soil as long as competition by terrestrial plants is low (“facultative epiphytes,” e.g., Dawson 1988). Similarly, a considerable number of terrestrial plant species may sporadically grow on living substrate as “accidental epiphytes” (Fig. 1.1, Zotz and List 2003). Thus, although it is rather straightforward to address an *individual plant* as epiphytic or not, a completely watertight definition for an *epiphytic species* is hard to impossible.

Ecological definitions should facilitate rather than complicate our understanding of scientific issues. Thus, considering the frequently continuous nature of ecological processes, categories can only partly capture and organize complexity and will frequently stay fuzzy at the edges. For example, epiphytes may sometimes use other objects as structural support (e.g., a powerline, Fig. 1.2, Wester and Zotz 2010), but in my opinion there is no need for additional terminology. Similarly, many other groups that share the same living space, such as mistletoes or lianas, are unambiguously excluded, but what about facultative epiphytes? Clearly, our definition does not spare us the linguistic problem that noun (“epiphyte”) and adjective (“epiphytic”) have a somewhat different emphasis: the exceptional “epiphytic” growth of an individual of a terrestrial species will hardly justify the label “epiphyte” for the entire species (Fig. 1.1). To mention a final aspect, mistletoes and other stem parasites may aptly be called “epiphytic” when contrasted with soil-rooted hemiparasites such as most members of the Orobanchaceae, but such parasites should undoubtedly be separated from true epiphytes. In my view, the main issue is

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Fig. 1.1 Epiphytic individuals of *Taraxacum campylodes* and *Sorbus aucuparia* in western Germany; a case of accidental epiphytism of otherwise terrestrial species (Photograph: Dirk Albach)

awareness of ecological distinctness irrespective of language, but unambiguous terminological clarity helps—dubbing mistletoes "aerial" hemiparasitic plants as done by Fadini and Cintra (2015) is a possible way to avoid confusion.

There are a number of more or less sophisticated schemes that have been proposed to tackle the problem of varying degrees of fidelity to the epiphytic lifestyle (Benzing 1990; Burns 2010; Ibisch 1996). For example, Ibisch (1996) distinguished "obligate" epiphytes (>95 % of all individuals in a particular region growing epiphytically) from "accidental" epiphytes (>95 % of all individuals in a region growing terrestrially) and "facultative" epiphytes (with proportions between these two extremes). Unfortunately, for most species the detailed information necessary to apply such a scheme is simply not available, and this situation will hardly change in the near future. Moreover, there can be regional variation in the degree of fidelity to the epiphytic habitat *within* a species. Sometimes such differences are not difficult to interpret, e.g., when *Brachyglottis kirkii* is almost exclusively growing as an epiphyte in damp forests, but is found as a terrestrial in dry forest in New Zealand (Oliver 1930). Today, the two forms are distinguished as distinct varieties of one species (Kirby 2014). In other cases, however, immediate explanations are wanting. The bromeliad *Vriesea arachnoidea*, for example, is

Fig. 1.2 Many epiphyte species are quite opportunistic in the choice of growing sites. (**a**) *Tillandsia flexuosa* on power lines Los Santos, lowland Panama. (**b**) Hyper-epiphyte *Tillandsia elongata* growing on epiphytic cactus near Santiago, Panama. (**c**) *Sedum* and polypod ferns on roof near Oaxaca, Mexico. (**d**) Epiphyll bromeliad on aroid leaf in Fortuna, Panama. (**e**) *Niphidium crassifolium* on rope on boat wreck near Barro Colorado Island, Panama (Photographs: Stefan Wester (**a**), Helena Einzmann (**b**))

primarily occupying tussocks on leaf litter in most of its natural range, but in the Serra da Araponga (Minas Gerais) this species is almost exclusively growing as epiphyte (Gomes-da-Silva and da Costa 2011). Finally, in very wet forests the distinction between epiphytes and terrestrials is inevitably vague, because growth conditions on moss-laden branches of stunted trees, e.g., in tropical elfin forests, hardly differ from those on moss-covered ground, a fact already mentioned by Schimper (1888).

1.2 Other Forms of Structurally Dependent Plants

Epiphytes are only one of several types of structurally dependent plant types (Fig. 1.3), and insights into the biology of the other types should also be instructive for our understanding of epiphytes and vice versa. Ignoring *parasitic* mistletoes, three additional groups are usually recognized. Apart from (1) climbing plants (*woody* "lianas" and *nonwoody* "vines"), which germinate on the ground and develop a flexible stem, most researchers are used to distinguish (2) "primary hemiepiphytes" and (3) "secondary hemiepiphytes." The former are characterized by an epiphytic stage before establishing root contact with the soil and the latter by terrestrial germination (Fig. 1.4), a vine-like stage, eventually with degeneration of the lower, proximal part of the shoot. The original definition of the latter emphasized the "loss of all connections with the ground" during ontogeny (Kress 1986; Putz and Holbrook 1986), but this crucial point has been frequently ignored in later applications of this concept and climbing plants with aerial feeder roots reaching the ground have routinely been called "secondary hemiepiphytes" (e.g., Balcázar Vargas and van Andel 2005). In fact, the mere existence of that label has lured many researchers (including the author of this book, e.g., Zotz and Vollrath 2003) into categorizing plants without appropriate scrutiny. We recently investigated several species of *Philodendron* and *Monstera*, which are usually

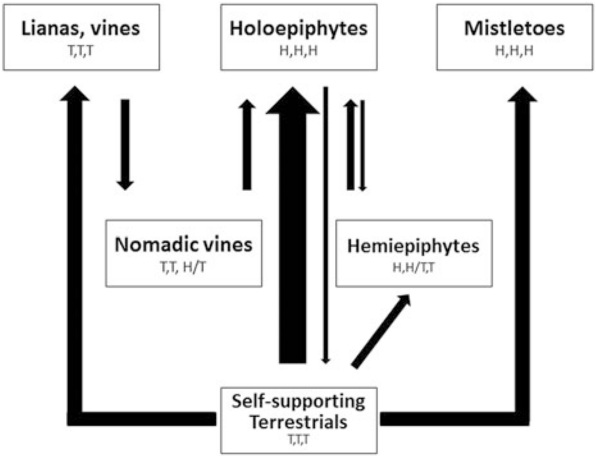

Fig. 1.3 Definitions and possible evolutionary connections (*arrows*) between different forms of structurally dependent plants. For each life form, the site of germination and the site of attachment of feeding roots during vegetative growth and during reproduction (*T* terrestrial, *H* Host tree) are given

Fig. 1.4 Nomadic vines. Seeds of *Monstera* sp. recently germinated on the ground, and seedlings are now growing toward and up a nearby tree trunk. Location: Las Cruces Biological Station, Costa Rica

labeled as secondary hemiepiphytes (Croat 1978; Williams-Linera and Lawton 1995), and checked whether these really fulfill Kress' (1986) definition. Examining hundreds of plants in the lowland forest of Barro Colorado Island, we found not a single large individual *without* root connections with the ground (M. Hüsener and G. Zotz, unpublished data)!

The use of "secondary hemiepiphyte" has been criticized almost from the start, interestingly also from those who have originally introduced the term (Holbrook and Putz 1996). I have recently suggested abandoning its usage entirely (Zotz 2013) in favor of the term "nomadic vine" (a term coined by Moffett 2000). This has many advantages: the new term does not imply a relationship with (primary) hemiepiphytes, which does not really exist, but rather points to the similarity with other climbing plants. It also avoids many untested assumptions of the traditional term. It allows for occasional germination in canopy soil and does neither imply nor discard a continuous root connection with the soil, which discontinues the quite frequent practice of making conjectures in this regard without data. In the long run, however, we should conduct detailed studies on the ontogeny of these plants and understand their biology. Only then should we decide which terminology best describes biological differences and similarities! For the time being, the suggested change also avoids the ambiguity associated with the occasional use of "hemiepiphyte" without modifier in the literature (e.g., Mucunguzi 2007). Lastly, the use of "nomadic vines" will probably keep researchers from lumping them with true epiphytes and (primary) hemiepiphytes. This has happened in many published inventories, disregarding their very different ecology. Such a lack of distinction now hampers generalizations in reviews and meta-analyses and also results in lack of attention to possibly interesting interactions, e.g., antagonisms, between lianas/nomadic vines and low-level epiphytes (Chap. 8).

Undoubtedly, nature frequently does not subscribe to the clear definitions of textbooks. However, the proposed scheme is flexible enough to accept cases where species do not neatly fit a single category. Aroids, for example, are known to be quite plastic, with adult individuals of the same species growing as true epiphyte or, alternatively, as hemiepiphyte or nomadic vine (Zotz 2004). Analyzing such diversity may actually reveal some interesting biology. Having a closer look at seemingly established "facts" is always a good practice. For example, it is usually assumed that hemiepiphytes only reproduce after establishing soil contact via aerial roots (Prósperi et al. 2001), but there are observations that, e.g., individuals of *Griselinia lucida* can already flower during their epiphytic stage (C. Kirby, pers. comm.). Acknowledging such a complex and continuous reality, this monograph uses four basic terms with unambiguous definitions of structurally dependent flora (Fig. 1.3): epiphytes, hemiepiphytes as originally defined by Schimper (1903), "nomadic vines" (Moffett 2000), and climbing plants sensu strictu (lianas and vines).

Although sometimes lumped with epiphytes (e.g., Assédé et al. 2012), mistletoes will not be treated in this monograph in any detail. These parasites are ecologically distinct from epiphytes in almost all aspects of their biology and are also isolated evolutionarily from all other structurally dependent plants. They are restricted to five families in the order Santalales (Vidal-Russell and Nickrent 2008), which has no nonparasitic epiphytic members. Similar to the evolutionary development from ground-rooted plants to life in trees in true epiphytes, epiphytic mistletoes evolved from terrestrial root or stem parasites. Among mistletoes, *Gaiadendron punctatum* is an interesting special case, which at least sometimes does not attack the tree, but parasitizes epiphytic ferns and epiphytic ericaceous shrubs (Kuijt 1963), and hence represents a borderline case for inclusion as an "epiphyte." There is only one other known case of such aerial hemiparasitism on epiphytes, *Pedicularis dendrothauma* (Orobanchaceae, Allard et al. 2005).

1.3 Other Classification Schemes

Epiphytes are a diverse group taxonomically, morphologically, and ecologically. Benzing (1990) has elaborated a number of classification schemes, which can be useful depending on the particular research question. Box 1.1 compiles these different schemes for easy reference.

Box 1.1 Different classification schemes for epiphytes (after Benzing 1990, modified)

I. *Relationships to the host*
  1. Accidental
  2. Facultative
  3. Hemiepiphytic
    3.1 Strangling
    3.2 Non-strangling
  4. Nomadic vines (only when shown to be disconnected to the ground)
  5. Genuinely epiphytic

(continued)

Box 1.1 (continued)

- II. *Growth habit*
  - 1. Trees
  - 2. Shrubs
  - 3. Suffrutescent to herbaceous forms
    - 3.1 Tuberous
      - 3.1.1 Storage, woody, and herbaceous
      - 3.1.2 Myrmecophytic, mostly herbaceous
    - 3.2 Broadly creeping: woody or herbaceous
    - 3.3 Narrowly creeping: mostly herbaceous
    - 3.4 Rosulate, herbaceous
    - 3.5 Root/leaf tangle, herbaceous
    - 3.6 Trash-basket, herbaceous
- III. *Humidity*
  - 1. Poikilohydrous (few species)
  - 2. Homoiohydrous
    - 2.1 Hygrophytes
    - 2.2 Mesophytes
    - 2.3 Xerophytes
      - 2.3.1 Drought endurers
      - 2.3.2 Drought avoiders
    - 2.4 Impounders
- IV. *Light (adapted from* Pittendrigh 1948*)*
  - 1. Exposure types
  - 2. Sun types
  - 3. Shade-tolerant types
- V. *Phorophyte-provided media*
  - 1. Relatively independent of rooting medium
    - 1.1 Atmospheric forms
    - 1.2 Twig and bark inhabitants
    - 1.3 Forms creating substitute soils or attracting ant colonies
  - 2. Utilizing preexisting specific rooting media
    - 2.1 Humus-dependent
      - 2.1.1 Shallow humus forms
      - 2.1.2 Deep humus forms
    - 2.2 Ant-nest garden and plant catchment inhabitants

1.4 Epiphytes: A Life Form?

Most researchers treat epiphytes as a life form, although Raunkiaer (1934) included epiphytes in the category “phanerophytes” in his original publication on plant life forms. During later revisions of the life form system, it has become customary to treat epiphytes as a distinct group. Since the life form concept aims at putting plant structure in an ecological context, a separation of mostly herbaceous epiphytes from trees is certainly more than appropriate. However, the use of terminology is not consistent, and “epiphytes” are also treated as growth habit or as growth form (e.g., Nadkarni and Haber 2009). Mori et al. (2002) argue that the defining characteristic of epiphytes is their habitat and suggest that epiphytes should be assigned to different life forms, e.g., shrubs, vines, or herbs. Acknowledging that the treatment of epiphytes as an independent life form has limitations, the advantages of a separate category arguably prevail. Life form spectra are a very useful way of comparing the structure of different vegetation types at a continental or global scale (Gentry and Dodson 1987). The so-called epiphyte quotient (EQ, Hosokawa 1950) focuses on epiphytes, being defined as the ratio of the number of epiphyte species to all other co-occurring species. The graphical representation of Hosokawa’s (1950) list of the EQs of 13 islands in the South Pacific (Fig. 1.5) immediately illustrates its usefulness for detecting ecological patterns and suggesting possible mechanistic explanations; e.g., the observed pattern represents a very early quantitative demonstration of the importance of moisture for vascular epiphytes.

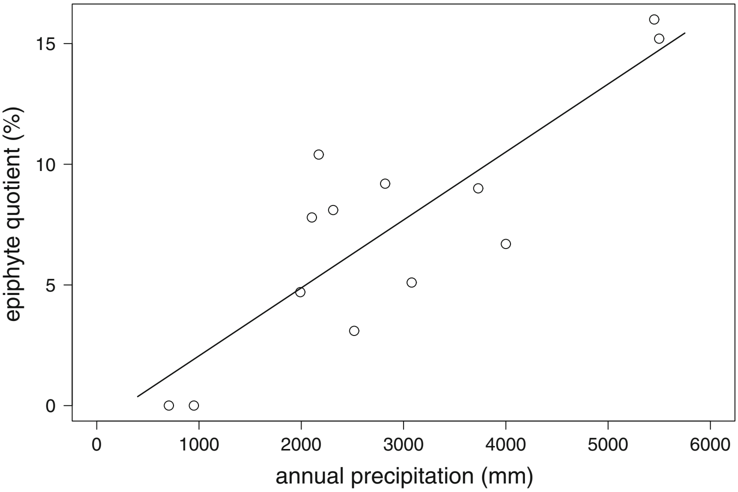

Fig. 1.5 Correlations of the epiphyte quotient (=the number of epiphyte species in relation to all vascular species) on 13 islands in the South Pacific and annual rainfall. A linear regression explains 72 % of the variation ($p > 0.001$). Data from the classic study of Hosokawa (1950)

1.5 Why Conquer Trees?

Going back to statements originally made by Schimper (1888), many general ecology texts state that epiphytes trade increased light availability for higher temperatures and low levels of water and nutrients (e.g., Huston 1994; Sitte et al. 2002; Osborne 2000). This is a rather simplistic picture because light conditions of epiphytes span the entire gradient from deep shade in the forest understory for species colonizing the lower portion of boles (e.g., many Hymenophyllaceae) to full radiation in the case of twig epiphytes (e.g., *Leochilus labiatus* or *Erycina pumilio*, Fig. 4.9, Chase 1987). Thus, epiphytism should better be conceptualized as the conquest of space as a previously unexploited resource (Lüttge 2008), with its intersecting and partially opposing gradients of light, temperature, humidity, and nutrient supply, and highly varying substrate characteristics related to tree architecture, bark structure, bark chemistry, or branch demography.

Table 1.1 summarizes possible mechanisms behind current epiphytic occurrences. Some mechanisms are *sufficient* to render any other but epiphytic growth in a forest impossible, others only *promote* vertical shifts. A certain degree of drought resistance seems to be necessary for all epiphytes, but besides this rather vaguely defined feature, it is difficult to find another characteristic that is *necessary* to thrive as an epiphyte. Not a single feature seems to be positively *sufficient*. Traits that allow a plant to cope with intermittent water supply may in turn impede growth under particular circumstances such as very wet conditions in the understory. A case in point would be the velamen radicum in orchids (Chap. 4) and another one thick layers of absorbing trichomes which when wet impede CO_2 diffusion in some bromeliads, i.e., so-called atmospherics. Many epiphytes may not tolerate shade, and low light in the understory could thus be another proximate cause for exclusively epiphytic existence of a species in a forest. For example, hemiepiphytic *Clusia uvitana* is never found growing terrestrially on Barro Colorado Island, Panama, with the exception of the rocky and exposed banks of Lake Gatun (Zotz, pers. obs.). An alternative explanation for the exclusion from terrestrial existence may be related to anatomy. Thick succulent roots of *Clusia* seedlings may be ideal

Table 1.1 Mechanisms potentially "explaining" epiphytic growth

Reasons primarily related to autoecology
1. Adaptations to drought that are incompatible with moist conditions [NT]
2. Intolerance to shade [P, NT]
3. Adaptations that allow anchorage to fissured bark, but not in soil [P, NT]
4. Pending plant body or pending inflorescences [NT]
Reasons primarily related to biotic interactions
5. Lack of resistance of pathogens in moist soil [NT]
6. Avoidance of competition (low growth rates, small stature make weak competitor) [NT]
7. Seed predation in soils and/or herbivore pressure [P]

Mechanisms directly *promoting* epiphytic existence [P] are distinguished from those that *preclude* terrestrial existence in a forest [NT] for securing establishment in fissured bark and storing water, but do not provide sufficient anchorage in soil: in an experiment, plantlets rooting in soil—unlike those rooting in bark—invariably tipped over during heavy rains and rotted (Zotz and Andrade 2002). Laman (1995) also showed that hemiepiphytic *Ficus crassiramea* subsp. *stupenda* germinates similarly well in moss, in rotten wood, and in soil, but further development in soil failed for unknown reasons. The development of pendant growth forms is likely to be an evolutionary dead end, because these are hardly compatible with terrestrial growth (Fig. 4.2). An alternative explanation for the failure to germinate and/or to grow terrestrially could be susceptibility to soil-bound pathogens. Experimental seedlings of hemiepiphytic *Ficus* species were all infected with fungi and died (Titus et al. 1990). Similarly, *Clusia uvitana* plantlets growing in unsterilized soil invariably succumbed to root rot (G. Zotz, unpubl. data). Ultimately, a key reason for epiphytic growth could be the avoidance of competition. All epiphyte species studied to date show very low inherent growth rates (Sect. 5.5) and generally small stature is another albeit largely untested attribute (Chap. 4). Both characteristics suggest that epiphytes are weak competitors. Noninhabitability of terrestrial sites is also suggested by findings of severe seed predation (Massa 1996) and herbivore pressure (Gaxiola et al. 2008): deer in New Zealand prevents almost all ground-level regeneration of facultative epiphytes. This involuntary experiment with an introduced herbivore could well mimic similar, natural processes in undisturbed forests.

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Epiphyte Taxonomy and Evolutionary Trends

2

2.1 Taxonomic Participation

Schimper (1888) supplied the first list of epiphytic taxa in his seminal work on vascular epiphytes of the New World with some information on other regions such as the Himalaya or New Zealand. Later efforts took advantage of an increasingly improved and accessible data basis and provided much more comprehensive, quantitative information with a global scope (Atwood 1986; Madison 1977; Renner 1986). For almost three decades, Kress (1986)'s compilation has been the standard reference of the taxonomic distribution of vascular epiphytes. This list counted some 23,000 species in 84 families as epiphytes. Recently, Zotz (2013) provided a revised list of the distribution of vascular epiphytes in the plant kingdom. This revision did not only incorporate all the changes in the grouping of extant plant life associated with the large-scale use of molecular techniques and included all new reports of epiphytic taxa during the last decades, but also introduced a more rigorous definition of the term "epiphyte" (Chap. 1). Treating the site of germination as critical feature automatically led to the exclusion of all nomadic vines (Putz and Holbrook 1986), which accounted for hundreds of species in Kress's list, particularly in the Araceae. In spite of such changes, the general description of the taxonomic affiliations of epiphytes within the plant kingdom by Kress (1986) and Benzing (1990) remains unaltered: epiphytism among vascular plants is particularly prevalent among ferns, virtually absent in gymnosperms, and highly dominated by monocotyledons within angiosperms (Magnoliidae) (Figs. 2.1, 2.2, and 2.3).

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Fig. 2.1 Representative examples of epiphytic members of the most important families of ferns and fern allies with >100 epiphytic species. (**a**) Polypodiaceae (*Microgramma*), (**b**) Aspleniaceae (*Asplenium*), (**c**) Dryopteridaceae (*Elaphoglossum*), (**d**) Hymenophyllaceae (*Hymenophyllum* and *Hymenoglossum*), (**e**) Lycopodiaceae (*Huperzia*), (**f**) Pteridaceae (*Vittaria*) (Photographs b: Michael Kessler, d: Simon Pflanzelt, c, e: Einzmann)

Fig. 2.2 Representative examples of epiphytic members of the most important angiosperm families with >200 epiphytic species. The shown families (genera) are (**a**) Orchidaceae (*Sobralia*), (**b**) Bromeliaceae (*Tillandsia*), (**c**) Piperaceae (*Peperomia*), (**d**) Ericaceae (*Macleania*), (**e**) Araceae (*Anthurium*), (**f**) Gesneriaceae (*Sarmienta*) (Photograph f: Alfredo Saldaña)

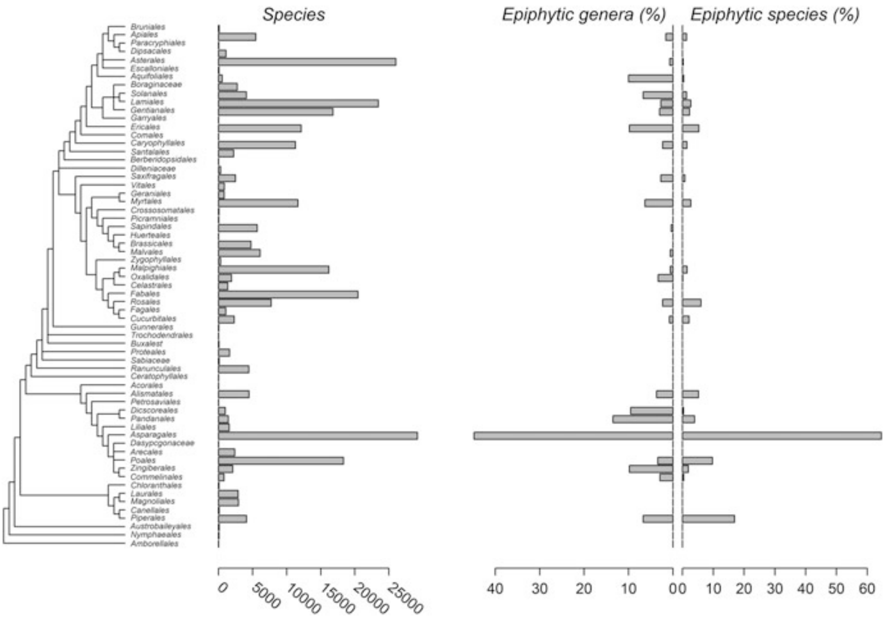


Fig. 2.3 Angiosperm phylogeny and contribution of different orders/families to epiphyte diversity. The cladogram on the *left* is based on the Angiosperm Phylogeny Group III system (http://www.mobot.org/MOBOT/research/APweb/). For each order/family, the total number of species is given (*bar chart* in the *center*) along with the proportion of epiphytic genera and species (*bar charts* on the *right*, data from Zotz 2013)

The list compiled by Zotz (2013) comprises almost 28,000 species of vascular epiphytes (including c. 800 species of hemiepiphytes in genera like *Ficus*, *Coussapoa*, or *Clusia*), representing 912 genera in 73 families, or about 9 % of all vascular plants (Table 2.1). The increase in species numbers of c. 5000 species compared to Kress (1986) can be largely explained by a similar increase in the numbers of known epiphytic orchids (Zotz 2013).

Table 2.1 Systematic distribution of vascular epiphytes

Taxa	Genera	Species
"Ferns and allies"	120/497	2864/11365
Subclass Lycopodiidae	4/5	223/807
Order Lycopodiales	3/3	214/430
Family Lycopodiaceae (F1)	3/3	214/430
Genus *Lycopodium* L.		3/46
Lycopodiella Holub s.l.		1/25
Huperzia Bernh. s.l.		210/339
Order Selaginellales	1/1	9/326
Family Selaginellaceae (F3)	1/1	9/326
Genus *Selaginella* Beauv. s.l.		9/326
Subclass Ophioglossidae	4/6	8/80
Order Ophioglossales	2/6	5/77
Family Ophioglossaceae (F5)	2/6	5/77
Genus *Botrychium* Sw.		3/45
Ophioglossum L.		2/20
Order Psilotales	2/2	3/3
Family Psilotaceae (F6)	2/2	3/3
Genus *Psilotum* Sw.		2/2
Tmesipteris Bernh.		1/1
Subclass Polypodiidae	112/469	2633/10273
Order Hymenophyllales	2/2	345/625
Family Hymenophyllaceae (F9)	2/2	345/625
Genus *Hymenophyllum* J. Sm. s.l.		195/300
Trichomanes L. s.l.		150/325
Order Schizaeales	1/10	2/104
Family Schizaeaceae (F14)	1/10	2/104
Genus *Schizaea* J. Sm.		2/13
Order Cyathales	1/4	1/458
Family Cyatheaceae (F23)	1/4	1/458
Genus *Cyathea* Sm.		1/284
Order Polypodiales	108/427	2285/8425
Family Lindsaeaceae (F29)	2/7	26/113
Genus *Lindsaea* Dryander ex J.Sm		25/80
Sphenomeris Maxon		1/12
Family Dennstaedtiaceae (F30)	2/10	2/246
Genus *Dennstaedtia* Bernh.		1/35
Microlepia Presl		1/81
Family Pteridaceae (F31)	17/53	107/1205
Genus *Ananthacorus* Underw.and Maxon		1/1
Anetium (Kunze) Splitg.		2/2
Antrophyum Kaulf.		17/17
Haplopteris Presl		23/24
Hecistopteris J.Sm.		2/2
Monogramma Schkurh.		6/6
Oetosis Neck. ex Greene		1/1
Pleurofossa Nakai ex H. Ito		1/1
Polytaenium Desv.		8/8
Pteropsis Desv.		1/1
Radiovittaria (Benedict) E.H. Crane		8/8
Rheopteris Alston		1/1
Scoliosorus Moore		3/3
Taeniopsis J. Sm.		1/1
Vaginopteris T. Nagai		1/1
Vaginularia Fee		2/2
Vittaria J.Sm.		29/29
Family Aspleniaceae (F33)	2/2	408/730
Genus *Asplenium* L.		400/700
Hymenasplenium Hayata		8/30
Family Dryopteridaceae (F42)	4/34	404/2023

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Genus *Elaphoglossum* Schott		400/600
Polystichum Roth		2/247
Revwattsia Jones		1/1
Rumohra Raddi		1/3
Family Lomariopsidaceae (F43)	1/14	2/553
Genus *Lomariopsis* Fee		2/31
Family Nephrolepidaceae (F44)	1/1	10/15
Genus *Nephrolepis* Schott		10/15
Family Tectariaceae (F45)	2/10	8/230
Genus *Arthropteris* J.Sm.		7/8
Psammiosorus C. Chr.		1/1
Family Oleandraceae (F46)	1/1	7/14
Genus *Oleandra* Cav.		7/14
Family Davalliaceae (F47)	2/2	60/60
Genus *Davallia* S.Sm.		42/42
Davallodes (Copel.) Copel.		18/18
Family Polypodiaceae (F48)	74/105	1251/1441
Genus *Acrosorus* Copel.		10/10
Adenophorus Gaudich.		14/16
Aglaomorpha Schott		9/9
Alansmia Labiak		26/26
Anarthropteris Copel.		1/1
Arthromeris (Moore) J.Sm.		14/19
Ascogrammitis Sundue		17/17
Belvisia Mirbel		9/9
Calymmodon Presl		5/5
Campyloneurum Presl		45/45
Ceradenia L.E. Bishop		40/40
Christiopteris Copel.		2/2
Chrysogrammitis Parris		2/2
Cochlidium Kaulf.		12/12
Colysis Presl		2/27
Crypsinus Presl		15/15
Ctenopterella Parris		8/8
Ctenopteris Bl. ex Kunze		21/21
Dasygrammitis Parris		6/6
Dendroconche Copel.		1/1
Dicranoglossum J.Sm.		5/5
Dictymia J.Sm.		5/5
Drymotaenium Makino		1/1
Drynaria (Bory) J.Sm.		16/16
Enterosora Baker		13/13
Glyphotaenium J. Sm.		1/1
Goniophlebium (Bl.) Presl		11/11
Grammitis Sw.		88/88
Lecanopteris Reinw.		1/1
Lellingeria A.R. Sm. and R.C. Moran		50/55
Lemmaphyllum Presl		4/4
Lepisorus (Sm.) Ching		5/93
Leptochilus Kaulf.		1/20
Leucotrichum Labiak		5/5
Lomaphlebia J. Smith		1/1
Loxogramme (Bl.) Presl		22/22
Luisma M.T. Murillo and A.R. Sm.		1/1
Melpomene A.R. Sm.and R.C. Moran		21/21
Microgramma Presl		28/28
Micropolypodium Hayata		4/4
Microsorum Link		33/33
Moranopteris R.Y. Hirai and J. Prado		27/28

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Nematopteris Alderwerelt		1/1
Neocheiropteris C. Chr.		9/9
Neurodium Fee		1/1
Niphidium J.Sm.		10/10
Oleandropsis Copel.		1/1
Oreogrammitis Copel.		6/6
Paragramma (Bl.) Moore		1/1
Paraleptochilus Copel.		1/1
Pecluma M.G. Price		34/34
Photinopteris J. Sm.		1/1
Phymatopteris Pic. Serm.		31/58
Platycerium Desv.		9/9
Pleopeltis Kunth in HBK		53/53
Pleurosoriopsis Fomin		1/1
Polypodiastrum Ching		1/4
Polypodiopteris Reed		2/2
Polypodium L.		130/160
Prosaptia Presl		86/86
Pyrrosia Mirbel		62/62
Radiogrammitis Parris		32/32
Scleroglossum Alderwerelt		2/2
Selliguea Bory		35/36
Serpocaulon A.R. Sm.		40/40
Solanopteris Copel.		4/4
Stenofilix Nakai		1/1
Terpsichore A.R. Sm.		38/38
Themelium (T. Moore) Parris		1/1
Thylacopteris Kunze ex Mett		1/1
Tomophyllum (E. Fourn.) Parris		23/23
Xiphopterella Parris		6/6
Xiphopteris Kaulf.		15/15
Zygophlebia L.E. Bishop		11/11
"gymnosperms"	1/88	1/1088
Subclass Cycadidae	1/10	1/313
Order Cycadales	1/10	1/313
Family Zamiaceae (G1)	1/9	1/203
Genus *Zamia* L.		1/57
Subclass Magnoliidae ("angiosperms")	795/14038	24745/275027[a]
Order Piperales	1/15	693/4093
Family Piperaceae (12)	1/13	693/2674
Genus *Peperomia* Ruiz and Pav.		693/1600
Order Alismatales	6/162	231/4463
Family Araceae (30)	6/113	231/3174
Genus *Anthurium* Schott		188/862
Arisaema Schott		2/183
Philodendron Schott		23/447
Remusatia Schott		4/4
Scindapsus Schott		3/35
Stenospermation Schott		11/48
Order Dioscoreales	2/21	3/974
Family Burmanniaceae (45)	1/9	2/159
Genus *Burmannia* L.		2/57
Family Dioscoreaceae (46)	1/3	1/805
Genus *Dioscorea* L.		1/610
Order Pandanales	6/37	60/1425[a]
Family Cyclanthaceae (50)	5/12	55/230
Genus *Asplundia* Harling		5/100
Chorigyne R.Erikss.		7/7
Ludovia Brongn.		1/3

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Sphaeradenia Harling		40/52
Stelestylis Drude		2/4
Family Pandanaceae (51)	1/4	5/1062[a]
Genus *Pandanus* Park. *(Benstonea)*		5/746[a]
Order Liliales	1/67	2/1558[a]
Family Liliaceae (61)	1/15	2/610[a]
Genus Lilium L.		2/111[a]
Order Asparagales	544/1213	18876/29190[a]
Family Orchidaceae (62)	530/880	18839/27135[a]
Genus *Abdominea* J.J. Sm.		1/1
Acampe Lindl.		8/8
Acianthera Scheidw.		195/201[a]
Acineta Lindl.		17/17
Acostaea Schltr.		6/6
Acriopsis Reinw. ex Bl.		9/9
Acrochaene Lindl.		1/1
Acrorchis Dressl.		1/1
Ada Lindl.		3/3
Adamantinia Van den Berg and C.N. Gonç.		1/1
Adenoncos Bl.		18/18
Adrorhizon J.D. Hook.		1/1
Aerangis Rchb. f.		50/51
Aeranthes Lindl.		43/43
Aerides Lour.		25/25
Aetheorhyncha Dressl.		1/1
Aganisia Kaempf. ex Spreng.		3/3
Aglossorhyncha Schltr.		13/13
Agrostophyllum Bl.		91/91
Alamania La Ll. and Lex.		1/1
Alatiliparis Marg. and Szlach.		5/5
Ambrella H. Perrier		1/1
Amesiella Schltr. ex Garay		3/3
Amparoa Schltr.		1/1
Anathallis Barb. Rodr.		147/147
Ancistrochilus Rolfe		2/2
Ancistrorhynchus Finet		18/18
Andinia (Luer)Luer		13/13
Angraecopsis Krzl.		22/22
Angraecum Bory		209/221
Ansellia Lindl.		1/1
Appendicula Bl.		133/134
Arachnis Bl.		11/11
Archivea Christenson and Jenny		1/1
Armodorum Breda		4/4
Arnottia A.Rich.		1/4
Arpophyllum La Ll. and Lex.		3/3
Artorima Dressl. and Poll.		1/1
Ascidieria Seidenf.		5/5
Ascocentropsis Senghas and Schildh.		1/1
Ascocentrum Schltr.		13/13
Ascochilopsis Carr		2/2
Ascochilus Ridl.		6/6
Ascoglossum Schltr.		1/1
Aspasia Lindl.		7/7
Aspidogyne Garay		1/46
Barbosella Schltr.		19/19
Barkeria Knowles and Westc.		15/15
Batemannia Lindl.		5/5
Beclardia A. Rich.		2/2

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Beloglottis Schltr.		2/7
Benthamia A. Rich.		1/31
Benzingia Dodson ex Dodson		9/9
Biermannia King and Pantl.		11/11
Bifrenaria Lindl.		20/21
Bogoria J.J. Sm.		4/4
Bolusiella Schltr.		6/6
Brachionidium Lindl.		73/73
Brachtia Rchb. f.		7/7
Brachypeza Garay		7/7
Bracisepalum J.J. Sm.		2/2
Braemia Jenny		1/1
Brasiliorchis Singer, Kohler, Carnev.		13/13
Brassavola R. Br.		22/22
Brassia R. Br.		46/46
Bromheadia Lindl.		27/29[a]
Broughtonia R. Br.		6/6
Bryobium Lindl.		8/8
Bulbophyllum Thouars		1865/1866
Bulleyia Schltr.		1/1
Calanthe R. Br.		4/203
Callostylis Bl.		4/4
Caluera Dodson and Determann		3/3
Calymmanthera Schltr.		5/5
Calyptrochilum Krzl.		2/2
Camaridium Lindl.		81/81
Campanulorchis Brieger		4/4
Campylocentrum Benth.		64/64
Capanemia Barb. Rodr.		9/9
Cardiochilus Cribb.		1/1
Catasetum L.C. Rich. ex Kunth		170/176
Cattleya Lindl.		96/110
Caucaea Schltr.		9/9
Caularthron Raf.		4/4
Centroglossa Barb. Rodr.		5/5
Ceratocentron Senghas		1/1
Ceratochilus Bl.		1/1
Ceratostylis Bl.		145/145
Chamaeangis Schltr.		11/11
Chamaeanthus Schltr. ex J.J. Sm.		2/2
Chamelophyton Garay		1/1
Chaseella Summerh.		1/1
Chaubardia Rchb. f.		3/3
Chaubardiella Garay		8/8
Chauliodon Summerh.		1/1
Cheiradenia Lindl.		1/1
Cheirostylis Bl.		1/54
Chelonistele Pfitzer		13/13
Chilopogon Schltr.		2/2
Chiloschista Lindl.		20/20
Chondrorhyncha Lindl.		7/7
Chondroscaphe Dressl. (Senghas and G. Gerlach)		14/14
Christensonella Szlach. et al.		12/16
Christensonia Haager		1/1
Chroniochilus J.J. Sm.		5/5
Chrysoglossum Bl.		3/4
Chysis Lindl.		10/10
Chytroglossa Rchb. f.		3/3
Cirrhaea Lindl.		7/7

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Cischweinfia Dressl. and N. Wms.		10/10
Cladobium Lindl.		1/1
Cleisocentron Bruhl		5/5
Cleisomeria Lindl. ex G. Don		2/2
Cleisostoma Bl.		90/90
Cleisostomopsis Seidenfaden		2/2
Clowesia Lindl.		7/7
Cochleanthes Raf.		4/4
Coelia Lindl.		5/5
Coeliopsis Rchb. f.		1/1
Coelogyne Lindl.		189/198
Comparettia Poepp. and Endl.		77/77
Conchidium Griff.		9/10
Constantia Barb. Rodr.		3/6
Cordiglottis J.J. Sm.		7/7
Coryanthes W.J. Hook.		53/53
Cottonia Wight		1/1
Crepidium Bl.		3/260
Cribbia Senghas		4/4
Crossoglossa Dressl. and Dodson		1/26
Cryptarrhena Lindl.		3/3
Cryptocentrum Benth.		20/20
Cryptochilus Wall.		5/5
Cryptopus Lindl.		4/4
Cryptopylos Garay		1/1
Cuitlauzina La Llave and Lex.		7/7
Cyclopogon Presl		3/80
Cycnoches Lindl.		34/34
Cymbidiella Rolfe		3/3
Cymbidium Sw.		53/70
Cynorkis Thouars		1/156
Cypholoron Dodson and Dressl.		2/2
Cyrtidiorchis Rauschert		5/5
Cyrtochiloides N.H. Williams and M.W.Chase		3/3
Cyrtochilum Kunth		125/125
Cyrtopodium R.Br.		33/48
Cyrtorchis Schltr.		18/18
Daiotyla Dressl.		4/4
Deceptor Seidenf.		1/1
Dendrobium Sw.		1427/1448
Dendrochilum Bl.		270/273
Dendrophylax Rchb. f.		14/14
Devogelia Schuit.		1/1
Diaphananthe Schltr.		22/22
Dichaea Lindl.		119/119
Dickasonia L.O. Wms.		1/1
Dienia Lindl.		1/6
Dilochiopsis (Hook. F.) Brieger		1/1
Dilomilis Raf.		5/5
Dimerandra Schltr.		8/8
Dimorphorchis D. Don		5/5
Dinema Lindl.		1/1
Dinklageella Mansf.		3/4
Diodonopsis Pridgeon and M.W. Chase		5/5
Diplocentrum Lindl.		2/2
Diploprora J.D. Hook.		2/2
Dipodium R.Br.		22/24
Distylodon Summerh.		1/1
Domingoa Schltr.		2/4

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Draconanthes (Luer) Luer		2/2
Dracula Luer		127/127
Dresslerella Luer		13/13
Dressleria Dodson		11/11
Dryadella Luer		53/53
Dryadorchis Schltr.		5/5
Drymoanthus Nicholls		4/4
Drymoda Lindl.		3/3
Dyakia E.A. Christ, ined.		1/1
Earina Lindl.		7/7
Echinorhyncha Dressl.		5/5
Echinosepala Pridgeon and M.W. Chase		11/11
Eclecticus P.O'Byrne		1/1[a]
Eggelingia Summerh.		3/3
Elleanthus Presl		107/111
Eloyella P. Ortiz		7/7
Embreea Dodson		2/2
Encyclia W.J. Hook.		158/161
Entomophobia de Vogel		1/1
Eparmatostigma Garay		1/1
Epiblastus Schltr.		21/22
Epidendrum L.		1241/1374
Epilyna Schltr.		2/2
Erasanthe P.J.Cribb, Hermans and D.L.Roberts		1/1
Eria Lindl.		259/262
Eriodes Rolfe		1/1
Eriopsis Lindl.		4/5
Erycina Lindl.		7/7
Esmeralda Rchb. f.		3/3
Euanthe Schltr.		1/1
Eulophia R.Br. ex Lindl		2/197
Eulophiella Rolfe		3/5
Euryblema Dressl.		2/2
Eurychone Schltr.		2/2
Eurystyles Wawra		20/20
Fernandezia Ruiz and Pav.		10/10
Frondaria Luer		1/1
Galeandra Lindl.		34/38
Galeottia A. Rich. and Galeotti		12/12
Gastrochilus D. Don		55/56
Gastrorchis Schltr.		2/8
Geesinkorchis de Vogel		4/4
Genyorchis Schltr.		10/10
Glomera Bl.		131/131
Gomesa R.Br.		115/118
Gomphichis Lindl.		1/24
Gongora Ruiz and Pav.		74/74
Goodyera R.Br. in W.T.Aiton		3/99
Grammangis Rchb. f.		2/2
Grammatophyllum Bl.		12/12
Grandiphyllum Docha Neto		6/6
Graphorkis Thouars		4/4
Grobya Lindl.		5/5
Grosourdya Rchb. f.		9/9
Guarianthe Dressl. and W.E. Higgins		3/4
Gunnarella Senghas		9/9
Gynoglottis J.J. Sm.		1/1
Hagsatera G. Tomayo		2/2
Haraella Kudo		1/1

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Hedeorkis Thouars		2/2
Helleriella Hawkes		2/2
Heterotaxis Lindl.		13/13
Hintonella Ames		1/1
Hippeophyllum Schltr.		10/10
Hoehneella Ruschi		2/2
Hofmeisterella Rchb. f.		2/2
Holcoglossum Schltr.		13/13
Homalopetalum Rolfe		8/8
Horichia Jenny		1/1
Horvatia Garay		1/1
Houlletia Brongn.		8/9
Huntleya Batem. ex Lindl.		14/14
Hygrochilus Pfitz.		1/1
Hylaeorchis G.A.Romero and Carnevali		1/1
Hymenorchis Schltr.		11/11
India A.N. Rao		1/1
Ionopsis Kunth		6/6
Inti M.A.Blanco		2/2
Isabelia Barb. Rodr.		3/3
Ischnogyne Schltr.		1/1
Isochilus R.Br.		13/13
Ixyophora Dressl.		5/5
Jaquiniella Schltr.		12/12
Jejewoodia Szlach.		2/2
Jejosephia A.N.Rao and Mani		1/1
Jumellea Schltr.		57/61
Kefersteinia Rchb. f.		70/70
Kegeliella Mansf.		4/4
Kraenzlinella Kuntze		9/9
Lacaena Lindl.		2/2
Laelia Lindl.		24/24
Lankesterella Ames		11/11
Lemurella Schltr.		4/4
Lemurorchis Kraenzl.		1/1
Leochilus Knowles and Westc.		12/12
Lepanthes Sw.		1073/1073
Lepanthopsis Ames		43/43
Leptotes Lindl.		9/9
Liparis L.C. Rich.		363/433
Listrostachys Rchb. f.		1/1
Lockhartia W.J. Hook.		28/28
Loefgrenianthus Hoehne		1/1
Lueckelia Jenny		1/1
Lueddemannia Lind. and Rchb. f.		3/3
Luisia Gaud.		39/39
Lycaste Lindl.		31/31
Lycomormium Rchb. f.		5/5
Macradenia R.Br.		11/11
Macroclinium Dodson		40/40
Macropodanthus L.O. Wms.		5/5
Malaxis Sol. ex Sw.		4/182
Malleola J.J. Sm.		33/33
Mapinguari Carnevali and Singer		3/4
Margelliantha P.J.Cribb		6/6
Masdevallia Ruiz and Pav.		588/590
Maxillaria Ruiz and Pav.		307/314
Maxillariella M.A. Blanco and Carnevali		44/44
Mediocalcar J.J. Sm.		17/17

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Megalotus Garay		1/1
Meiracyllium Rchb. f.		2/2
Mesospinidium Rchb. f.		8/8
Microchilus C.Presl		1/136
Microcoelia Lindl.		30/30
Microepidendrum Brieger ex W.E. Higgins		1/1
Micropera Lindl.		21/21
Microsaccus Bl.		13/13
Microtatorchis Schltr.		51/51
Microterangis Senghas		7/7
Miltonia Lindl.		12/12
Miltoniopsis Godefr.-Lebeuf		5/5
Mobilabium Rupp		1/1
Monomeria Lindl.		2/2
Mormodes Lindl.		78/78
Mormolyca Fenzl		25/25
Mycaranthes Bl.		30/30
Myoxanthus Poepp. and Endl.		48/48
Myrmecophila Rolfe		10/10
Mystacidium Lindl.		10/10
Nabuluia Ames		3/3
Neobathiea Schltr.		5/5
Neocogniauxia Schltr.		2/2
Neofinetia Hu		3/3
Neogardneria Schltr.		1/1
Neogyna Rchb. f.		1/1
Neomoorea Rolfe		1/1
Nephrangis Summerh.		2/2
Nidema Britt. and Millsp.		2/2
Nitidobulbon Ojeda, Carnevali and G.A.Romero		3/3
Nohawilliamsia M.W.Chase and Whitten		1/1
Notheria O'Byrne and J.J.Verm.		1/1
Nothodoritis Z.H.Tsi		1/1
Notylia Lindl.		56/56
Notyliopsis P.Ortiz		1/1
Oberonia Lindl.		317/319
Octarrhena Thwaites		52/52
Octomeria R.Br.		146/149
Oeoniella Schltr.		2/2
Oeonia Lindl.		5/5
Oestlundia W.E. Higgins		4/4
Oliveriana Rchb. f.		6/6
Omoea Bl.		2/2
Oncidium Sw.		303/310
Ophioglossella Schuit. and Ormerod		1/1
Orleanesia Barb. Rodr.		9/9
Ornithidium R. Br.		53/57
Ornithocephalus W.J. Hook.		52/52
Ornithochilus Wall. ex Lindl.		3/3
Ossiculum P.J.Cribb and Laan		1/1
Otochilus Lindl.		5/5
Otoglossum (Schltr.) Garay and Dunsterv.		13/13
Otostylis Schltr.		1/4
Oxystophyllum Bl.		36/36
Pabstia Garay		5/5
Pabstiella Brieger and Senghas		21/22
Pachyphyllum Kunth		39/39
Panisea Lindl.		9/10
Paphinia Lindl.		16/16

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Paphiopedilum Pfitz.		5/107
Papilionanthe Schltr.		9/11
Papillilabium Dockr.		1/1
Paralophia P.J.Cribb and Hermans		2/2
Paraphalaenopsis Hawkes		4/4
Parapteroceras Averyanov		8/8
Pedilochilus Schltr.		36/36
Pelatantheria Ridl.		8/8
Pelexia Pot. ex Lindl.		1/78
Penkimia Phukan and Odyuo		1/1
Pennilabium J.J. Sm.		13/13
Peristeranthus T.E. Hunt		1/1
Peristeria W.J. Hook.		13/13
Pescatoria Rchb. f.		25/25
Phalaenopsis Bl.		58/61[a]
Phloeophila Hoehne and Schltr.		11/11
Pholidota Lindl. Ex W.J. Hook.		38/39
Phragmipedium Rolfe		4/24
Phragmorchis L.O. Wms.		1/1
Phreatia Lindl.		211/211
Phymatidium Lindl.		10/10
Physoceras Schltr.		1/12
Pinalia Lindl.		77/79
Pityphyllum Schltr.		5/5
Platanthera Rich.		1/136
Platyrhiza Barb. Rodr.		1/1
Platystele Schltr.		99/99
Plectorrhiza Dockr.		3/3
Plectrelminthus Raf.		1/1
Plectrophora Focke		10/10
Pleione D.Don		6/26
Pleurothallopsis Porto and Brade		16/16
Pleurothallis R.Br.		566/566
Pleurothallopsis Porto and Brade		16/16
Poaephyllum Ridl.		6/6
Podangis Schltr.		1/1
Podochilus Bl.		61/62
Polycycnis Rchb. f.		15/17
Polyotidium Garay		1/1
Polystachya W.J. Hook.		237/244
Pomatocalpa Breda		25/25
Ponera Lindl.		8/8
Porpax Lindl.		13/13
Porphyrodesme Schltr.		3/3
Porphyroglottis Ridl.		1/1
Porroglossum Schltr.		41/41
Porrorhachis Garay		2/2
Promenaea Lindl.		18/18
Prosthechea Knowles and Westc.		115/120
Pseuderia Schltr.		20/20
Pseudocentrum Lindl.		1/7
Pseudolaelia Campos-Porto and Brade		15/15
Psychilis Raf.		15/15
Psychopsis Raf.		5/5
Pteroceras Hasselt ex Hassk.		26/26
Pterostemma Krzl.		3/3
Pygmaeorchis Brade		2/2
Quekettia Lindl.		5/5
Quisqueya D. Dod		3/4

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Rangaeris Summerh.		7/7
Rauhiella Pabst and Braga		3/3
Raycadenco Dodson		1/1
Renanthera Lour.		20/20[a]
Restrepia Kunth		53/53
Restrepiella Garay and Dunsterv.		2/2
Rhaesteria Summerh.		1/1
Rhetinantha M.A. Blanco		14/14
Rhinerrhiza Rupp		1/1
Rhinerrhizopsis Ormerod		3/3
Rhipidoglossum Schltr.		35/35
Rhynchogyna Seidenf. and Garay		3/3
Rhyncholaelia Schltr.		2/2
Rhynchostele Rchb.f.		15/17
Rhynchostylis Bl.		3/3
Ridleyella Schltr.		1/1
Robiquetia Gaud.		44/44
Rodriguezia Ruiz and Pav.		48/48
Rossioglossum (Schltr.) Garay and Kennedy		9/9
Rudolfiella Hoehne		6/6
Saccoglossum Schltr.		5/5
Saccolabiopsis J.J. Sm.		14/14
Saccolabium Bl.		5/5
Samarorchis Ormerod		1/1
Sanderella O. Ktze.		2/2
Santotomasia Ormerod		1/1
Sarcanthopsis Garay		5/5
Sarcochilus R.Br.		25/25
Sarcoglyphis Garay		12/12
Sarcophyton Garay		3/3
Sarcostoma Bl.		5/5
Saundersia Rchb. f.		2/2
Sauvetrea Szlach.		11/11
Scaphosepalum Pfitz.		46/46
Scaphyglottis Poepp. and Endl.		68/68
Schistotylus Dockr.		1/1
Schlimia Planch and Lind. ex Lindl. and Paxt.		7/7
Schoenorchis Bl.		24/24
Schunkea Senghas		1/1
Scuticaria Lindl.		9/10
Sedirea Garay and Sweet		2/2
Seegeriella Senghas		2/2
Seidenfadenia Garay		1/1
Seidenfadeniella C.S. Kumar		2/2
Sievekingia Rchb. f.		16/16
Singchia Z.J.Liu and L.J.Chen		1/1
Sirhookera O. Ktze.		2/2
Smithsonia Saldanha		3/3
Smitinandia Holtt.		3/3
Sobennikoffia Schltr.		2/4
Sobralia Ruiz and Pav.		12/146
Solenangis Schltr.		8/8
Solenidium Lindl.		3/3
Soterosanthus F.Lehm. ex Jenny		1/1
Specklinia Lindl.		134/134
Sphyrarhynchus Mansfeld		1/1
Spongiola J.J.Wood and A.L.Lamb		1/1
Stalkya Garay		1/1
Stanhopea Forst ex W.J. Hook.		61/61

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Staurochilus Ridl.		14/14
Stelis Sw.		882/884
Stenia Lindl.		22/22
Stenorrhynchos L.C. Rich.		1/5
Stereochilus Lindl.		7/7
Stichorkis Thouars		1/1
Stolzia Schltr.		15/15
Suarezia Dodson		1/1
Sudamerlycaste Archila		24/41
Summerhayesia Cribb.		2/2
Sunipia Buc.-Ham. ex J.E. Sm.		23/23
Sutrina Lindl.		2/2
Svenkoeltzia Burns-Bal		1/3
Systeloglossum Schltr.		5/5
Taeniophyllum Bl.		184/184
Taeniorrhiza Summerh.		1/1
Tainia Bl.		1/34
Teagueia Luer and Hirtz		11/11
Telipogon Kunth		205/205
Tetramicra Lindl.		1/14
Teuscheria Garay		7/7
Thecopus Seidenf.		2/2
Thecostele Rchb. f.		1/1
Thelasis Bl.		26/26
Thrixspermum Lour.		153/153
Thunia Rchb.f.		2/5
Thysanoglossa Porto and Brade		2/2
Ticoglossum Lucas Rodr. ex Halb.		2/2
Tipularia Nutt.		1/7
Tolumnia Raf.		25/25
Tomzanonia Nir		1/1
Trevoria Lehmann		5/5
Trias Lindl.		13/13
Triceratorhynchus Summerh.		1/1
Trichocentrum Poepp. and Endl.		70/70
Trichoceros Kunth		10/10
Trichoglottis Bl.		68/68
Trichopilia Lindl.		42/42
Trichosalpinx Luer		111/111
Trichotosia Bl.		78/78
Tridactyle Schltr.		47/47
Trigonidium Lindl.		13/13
Trisetella Luer		23/23
Trizeuxis Lindl.		1/1
Tuberolabium Yamamoto		17/17
Uncifera Lindl.		6/6
Vanda Jones		55/55
Vandopis Pfitz.		2/4
Vanilla Plumier ex Miller		1/103
Vasqueziella Dodson		1/1
Ventricularia Garay		2/2
Vitekorchis Romowicz and Szlach.		4/4
Warmingia Rchb. f.		4/4
Warczewiczella Rchb.f.		11/11
Warrea Lindl.		3/3
Warreella Schltr.		2/2
Warreopsis Garay		4/4
Xenikophyton Garay		2/2
Xylobium Lindl.		30/30

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Ypsilopus Summerh.		5/5
Ypsilorchis (Finet) Z.J.Liu, S.C.Chen and L.J.Chen		1/1
Zelenkoa M.W.Chase and N.H.Williams		1/1
Zootrophion Luer		22/22
Zygopetalum W.J. Hook.		11/15
Zygosepalum Rchb. f.		8/8
Zygostates Lindl.		22/22
Family Asteliaceae (65)	2/4	5/36
Genus *Astelia* Banks and Soland.		4/26
Collospermum Skotts.		5/5
Family Xanthorrhoeaceae	1/24	2/456
Genus Dianella Lam.		1/41
Family Amaryllidaceae (74)	5/79	11/2164
Genus *Clivia* Lindl.		1/7
Cyrtanthus Ait.		1/56
Hippeastrum Herb.		5/91
Pamianthe Stapf		3/3
Scadoxus Raf.		1/9
Family Asparagaceae (75)	7/143	20/3632[a]
Genus *Drimia* H. Perrier		1/99
Maianthemum F.H. Wigg.		6/39
Agave L.		2/196
Asparagus L.		1/209
Heteropolygonatum M.N.Tamura and Ogisu		6/6[a]
Polygonatum Mill.		3/71
Yucca L.		1/50
Order Commelinales	2/68	3/812
Family Commelinaceae (78)	2/41	3/723
Genus *Belosynapsis* Hassk.		1/6
Cochliostema Lem.		2/2
Order Zingiberales	9/92	39/2073
Family Costaceae (88)	1/4	3/110
Genus *Costus* L.		3/104
Family Zingiberaceae (89)	8/49	36/1187
Genus *Alpinia* Roxb.		1/241
Amomum Roxb.		4/176
Burbidgea J.D. Hook.		5/5
Cautleya Royle		4/4
Globba L.		1/96
Hedychium Koen.		16/87
Riedelia Oliv.		1/75
Rhynchanthus Hook f.		4/4
Order Poales	32/934	1778/18328
Family Bromeliaceae (92)	28/50	1770/3160
Genus Aechmea Ruiz and Pav.		255/268
Androlepis Brongn. ex Houllet		1/1
Araeococcus Brongn.		9/9
Billbergia Thunb.		64/65
Brocchinia Schult. f.		5/20
Bromelia L.		3/59
Canistrum E. Morr.		21/21
Catopsis Griseb.		19/21
Connellia N.E. Br.		1/6
Disteganthus Lem.		3/3
Fascicularia Mez		1/2
Fernseea Baker		1/2
Glomeropitcairnia Mez		2/2
Greigia Regel		1/32
Guzmania Ruiz and Pav.		181/212

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Hohenbergia Bak.		40/52
Hohenbergiopsis L.B. Sm. and R. Read		1/1
Lymania R. Read		8/9
Mezobromelia L.B. Sm. and R. Read		8/8
Navia J.H. Schult.		4/93
Neoregelia L.B. Sm.		109/115
Nidularium Lem.		40/50
Pitcairnia L Herit.		33/391
Portea Brongn. and. C. Koch		2/8
Quesnelia Gaudich		17/18
Ronnbergia E. Morren and André		12/12
Tillandsia L.		635/671
Vriesea Lindl.		294/340
Family Rapateaceae (93)	2/16	6/94
Genus *Epidryos* Maguire		3/3
Stegolepis Kl. ex. Koern.		3/33
Family Cyperaceae (99)	1/98	1/4350
Genus *Coleochloa* Gilly		1/8
Family Poaceae (106)	1/668	1/10025
Genus *Tripogon* Roem.and Schult.		1/39
Order Saxifragales	3/113	20/2476
Family Crassulaceae (134)	3/34	20/1370
Genus *Echeveria* DC.		8/167
Kalanchoe Adans		6/73
Sedum L.		6/348
Order Rosales	6/259	459/7708
Family Moraceae (154)	1/38	396/1100
Genus *Ficus* L.		396/830 (**H**)
Family Urticaceae (155)	5/54	63/2625
Genus *Coussapoa* Aubl.		25/48 (**H**)
Elatostema Gaudich.		12/512
Pilea Lindl.		20/225
Poikilospermum Zipp. ex Miq.		4/4 (**H**)
Procris Comm. Ex Juss.		2/2
Order Cucurbitales	1/129	49/2295
Family Begoniaceae (170)	1/2	49/1528
Genus *Begonia* L.		49/1528
Order Oxalidales	2/60	2/1914
Family Cunoninaceae (176)	1/26	2/280
Genus *Weinmannia* L.		2/81 (**H**)
Order Malpighiales	4/721	241/ 16189[a]
Family Calophyllaceae (210)	1/12	9/460[a]
Genus *Clusiella* Planch.and Triana		9/9
Family Clusiaceae (211)	3/14	232/595
Genus *Clusia* L.		230/306 (**H**)
Havetiopsis Planch. and Triana		1/2 (**H**)
Quapoya Aubl.		1/5 (**H**)
Order Myrtales	26/415	313/11651
Family Myrtaceae (222)	1/131	3/4625
Genus *Metrosideros* Banks ex Gaertn.		3/55 (**H**)
Family Onagraceae (220)	1/24	9/650
Genus *Fuchsia* L.		9/114
Family Melastomataceae (223)	23/188	300/4305
Genus *Adelobotrys* DC.		21/26
Blakea P.Br.		76/79
Calvoa J.D. Hook.		5/6
Catanthera F. Muell.		9/11
Clidemia D. Don		12/153
Dicellandra J.D. Hook.		1/1

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Graffenrieda DC.		2/50
Gravesia Naud		2/26
Hypenanthe Bl.		4/4
Kendrickia J.D. Hook.		1/1
Leandra Raddi		4/120
Medinilla Gaudich.		70/400
Miconia Ruiz and Pav.		13/709
Monolena Triana		8/8
Ossaea DC.		2/36
Pachycentria Bl.		6/8
Phainantha Glaeson		4/4
Plethiandra J.D. Hook.		8/8
Pleiochiton Naud. ex Miq.		7/7
Pogonanthera Bl.		1/1
Preussiella Gilg		1/1
Topobea Aubl.		41/47(**H**)
Triolena Naud.		2/20
Family Alzateaceae (225)	1/1	1/1
Genus Alzatea Ruiz and Pav.		1/1 (**H**)
Order Sapindales	2/461	2/5673
Family Burseraceae (238)	1/18	1/550 (**H**)
Genus *Bursera* Jacq. ex L.		1/120 (**H**)
Family Anacardiaceae (239)	1/70	1/985
Genus *Spondias* L.		1/7 (**H**)
Order Malvales	2/338	3/6093 (**H**)
Family Malvaceae (250)	2/243	3/4225
Genus *Ceiba* Mill.		2/20 (**H**)
Spirotheca Ulbrich		1/1 (**H**)
Order Caryophyllales	16/692	158/11278
Family Nepenthaceae (288)	1/1	34/104
Genus *Nepenthes* L.		34/104[a]
Family Cactaceae (316)	15/125	124/1432
Genus *Disocactus* Lindl.		11/11
Epiphyllum Haworth		12/12
Hatiora Britton and Rose		4/5
Hylocereus (Berg.) Britton and Rose		14/14
Lepismium Pfeiff.		6/6
Lymanbensonia Kimnach		3/4
Pfeiffera Salm-Dyck		6/6
Pseudorhipsalis Britton and Rose		6/6
Rhipsalidopsis Britton and Rose		2/2
Rhipsalis Gaertn.		33/35
Schlumbergera Lem.		5/6
Selenicereus (Berg.) Britton and Rose		12/12
Strophocactus Britton and Rose		1/3
Trichocereus (Berg.) Riccob.		1/9
Weberocereus Britton and Rose		8/8
Order Ericales	35/346	638/12112[a]
Family Balsaminaceae (323)	1/2	15/1001
Genus *Impatiens* L.		15/1000
Family Marcgraviaceae (324)	1/8	2/137[a]
Genus *Marcgravia* L.		2/62[a]
Family Primulaceae (333)	1/58	7/2590
Genus *Cybianthus* Mart.		7/161
Family Ericaceae (344)	32/126	629/3995
Genus Agapetes D.Don ex G. Don		75/147
Anthopteropsis A.C. Sm.		1/1
Anthopterus W.J. Hook.		3/12
Calopteryx A.C. Sm.		1/2

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Cavendishia Lindl.		82/113
Ceratostema Juss.		26/35
Costera J.J. Sm.		8/10
Demosthenesia A.C. Sm.		3/12
Didonica Luteyn and Wilbur		4/4
Dimorphanthera F. Muell.		13/77
Diogenesia Sleum.		4/13
Diplycosia Bl.		70/110
Disterigma Niedenzu ex Drude		18/40
Gaultheria Kalm ex L.		2/144
Gonocalyx Planch. and Lind.Ex A.C.Sm.		4/11
Lateropora A.C. Sm.		2/3
Lebetanthus Endl.		1/1
Macleania W.J. Hook.		19/28
Mycerinus A.C. Sm.		1/3
Oreanthes Benth.		7/7
Orthaea Kl.		9/25
Psammisia Kl.		30/39
Rhododendron L.		139/613
Rusbya Britton		1/1
Satyria Kl.		8/12
Semiramisa Kl.		1/2
Siphonandra Kl.		1/1
Sphyrospermum Poepp. and Endl.		18/22
Themistoclesia Kl.		14/17
Thibaudia Ruiz and Pav.		14/55
Utleya Wilbur and Luteyn		1/1
Vaccinium L.		49/172
Order Gentianales	33/1118	386/16787
Family Rubiaceae (350)	22/204	204/13548
Genus *Aidia* Lour.		1/53
Anthorrhiza C.R.Huxley and Jebb		8/8
Argostemma Wall.		2/161
Balmea Martinez		1/1
Chassalia Comm. ex J. L. M. Poiret		3/108
Coprosma J.R. and G. Forst.		2/116
Cosmibuena Ruiz and Pav.		2/4 (**H**)
Didymochlamys J.D. Hook.		2/2
Gardenia J. Ellis		1/143
Hillia Jacq.		20/25
Hoffmannia Sw.		2/118
Hydnophytum Jack		94/94
Hymenodictyon Wall.		2/23
Lecananthus Jack		3/3
Leucocodon G. Gardner		1/1
Mussaenda L.		1/195
Myrmecodia Jack		27/27
Myrmephytum Becc.		5/5
Notopleura (Oerst.) Bremek.		11/101
Psychotria L.		5/1907
Schradera Vahl		7/55
Squamellaria Becc.		4/4
Timonius DC.		1/168
Family Gentianaceae (351)	2/87	26/1650
Genus *Fagraea* Thunb.		23/72 (**H**)
Macrocarpaea Gilg		3/31
Family Apocynaceae (354)	9/415	156/4705
Genus *Absolmsia* Kuntze		1/1
Anatropanthus Schltr.		1/1

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Dischidia R.Br.		80/116
Dischidiopsis Schlecht.		8/8
Epistemma D.V. Field and J.B. Hall		3/4
Heynella Backer		1/1
Hoya R.Br.		60/200
Mandevilla Lindl.		4/188
Micholitzia N.E. Br.		1/1
Oreosparte Schltr.		1/1
Sarcorrhiza Bullock		1/1
Order Solanales	11/164	51/4079
Family Solanaceae (358)	11/102	51/2460
Genus *Dyssochroma* Miers		2/2
Hawkesiophyton A.T. Hunz.		3/3
Juanulloa Ruiz and Pav.		8/9
Lycianthes Hassl.		4/130
Markea L.C. Rich.		13/13 (**H**)
Merinthopodium Donn. Sm.		3/3
Rahowardiana D Arcy		1/1
Schultesianthus A.T. Hunz.		7/7
Solandra Sw.		3/9
Solanum L.		4/747
Trianaea Planch. and Linden		5/5
Order Lamiales	29/1058	631/23456
Family Gesneriaceae (367)	20/147	570/3990
Genus *Aeschynanthus* Jack		186/191
Agalmyla Bl.		90/96
Capanea Planch.		2/2
Codonanthe (Mart.) Hanst.		20/20
Codonanthopsis Mansf.		4/4
Columnea L.		192/197
Drymonia Mart.		8/71
Episcia Mart.		2/12
Fieldia A. Cunn.		1/2
Heppiella Regel		1/4
Loxostigma C.B. Cl.		3/7
Lysionotus G. Don		12/23
Nematanthus Schrader		22/28
Neomortonia Wiehler		2/2
Oerstedina Wiehler		3/3
Paradrymonia Hanst.		7/29
Rufodorsia Wiehler		5/5
Sarmienta Ruiz and Pav.		1/1
Sinningia Nees		4/60
Streptocarpus Lindl.		5/135
Family Scrophulariaceae (369)	1/87	1/985
Genus *Dermatobotrys* Bolus		1/1
Family Paulowniaceae (375)	1/3	1/19
Genus *Wightia* Wall.		1/1 (**H**)
Family Orobanchaceae (376)	1/80	1/1570
Genus *Pedicularis* L.		1/390
Family Lentibulariaceae (377)	2/3	18/320
Genus *Pinguicula* L.		4/49
Utricularia L.		14/146
Family Acanthaceae (378)	2/229	2/3500
Genus *Hansteinia* Oerst.		1/6
Louteridium S. Watson		1/6
Family Schlegeliaceae (381)	2/4	15/68
Genus *Gibsoniothamnus* L.O. Williams		12/12
Schlegelia Miq.		3/23

(continued)

Table 2.1 (continued)

Taxa	Genera	Species
Order Aquifoliales	2/20	2/535
Family Phyllonomaceae (387)	1/1	1/150
Genus *Phyllonoma* Willd. Ex Schult.		1/4
Family Aquifoliaceae (389)	1/1	1/405
Genus *Ilex* L.		1/414 (**H**)
Order Asterales	13/1744	58/26015
Family Campanulaceae (391)	5/84	20/2380
Genus *Burmeistera* Karst. and Triana		11/102
Canarina L.		1/3
Centropogon Presl		7/215
Clermontia Gaudich.		1/24
Trematolobelia Zahlbr. ex Rock.		1/7
Family Asteraceae (400)	8/1620	38/22750
Genus *Brachyglottis* J.R. Forst. and G. Forst.		1/39
Dahlia Cav.		1/38
Eupatorium L. (s.l.)		7/254
Neomirandea R.M. King and H. Rob.		21/28
Pentacalia Cass.		3/210
Sinclairia Hook and Arn.		2/28
Solanecio (Sch. Bip.) Walp.		1/16
Tuberostylis Steez		2/2
Order Apiales	8/494	71/5469
Family Griseliniaceae (409)	1/1	2/7
Genus *Griselinia* G. Forst.		2/7 (**H**)
Family Pittosporaceae (410)	1/9	2/200
Genus *Pittosporum* Banks ex Soland.		2/69 (**H**)
Family Araliaceae (411)	6/43	67/1450
Genus *Aralia* L.		6/72
Oreopanax Decne. and Planch		13/148 (**H**)
Pentapanax Seem.		1/1
Polyscias J.R. and G. Forst.		3/117 (**H**)
Pseudopanax C. Koch		2/7 (**H**)
Schefflera J.R. and G. Forst.		42/586 (**H**)

The compilation follows Zotz (2013), with a few corrections (indicated by [a]). For example, new unambiguous evidence required the inclusion of three additional families (Pandanaceae, Liliaceae, and Marcgraviaceae), and errors in the consulted databases in regard to the numbers of epiphytic species in the orchid genera *Bromheadia*, *Eclecticus*, and *Renanthera* are now corrected. Ignoring these changes and others, which will be necessary in the course of the continuous update of the epiphyte list, I opted to use the metrics of the original publication throughout the text. For each subclass in the table, order and family, the numbers of epiphytic genera/all genera, and numbers of epiphytic species/total species are given. Analogously, for each genus with epiphytic members the numbers of epiphytic species/total species are given. Numbers in parentheses behind the family names refer to the linear system as described in Christenhusz et al. (2011b: F1–F48), Christenhusz et al. (2011a: G1) and Haston et al. (2009: 1–411), respectively. An (H) marks genera that have primarily or only hemiepiphytes

2.1.1 Plant Families with a Substantial Number of Vascular Epiphytes

The distribution of epiphytes among the 11 currently accepted subclasses of vascular land plants (Chase and Reveal 2009) is very uneven. No epiphytes are known for the five subclasses Equisetidae, Marattiidae, Ginkgooidae, Pinidae, and Gnetidae, and there is only a single epiphytic species in Cycadidae, *Zamia pseudoparasitica*. In contrast, >25 % of Polypodiidae and about 9 % of Magnoliidae share a primarily epiphytic existence. In the following account, which largely follows Zotz (2013), all 29 families of vascular plants with at least 30 epiphytic species are briefly described.

About 2700 species in some 120 genera of ferns and fern allies are epiphytic (Table 2.1). Seven families have more than 30 epiphytic species. Polypodiaceae is by far the most important with 74 genera containing epiphytes, representing c. 50 % of all epiphytic fern species, although the fern genera with the largest number of epiphytic members are found in the families Aspleniaceae and Dryopteridaceae: the genera *Asplenium* and *Elaphoglossum* have more than 400 epiphytic species each. Three other genera in the family Dryopteridaceae have epiphytic members: a few facultatively epiphytic species in the genera *Ruhmora* and *Polystichum* and the monotypic rainforest epiphyte *Revwattsia fragilis*, endemic to Queensland, Australia. More than 300 Hymenophyllaceae species are epiphytic. The two traditionally accepted genera, *Hymenophyllum s.l.* and *Trichomanes s.l.*, corresponding to two phylogenetic lineages, have a large proportion of species found on trees (Dubuisson et al. 2003, 2009), although many of these taxa occur both as epiphyte and lithophyte (Box 2.1). Slightly fewer epiphytic species (c. 220 taxa) are found in Lycopodiaceae. Following generic delimitations of Christenhusz et al. (2011b), the three genera *Lycopodium, Lycopodiella*, and *Huperzia* are accepted: virtually all epiphytic species belong to the genus *Huperzia s.l.* The estimated 100 epiphytic species in Pteridaceae belong almost entirely to the subfamily Vittarioideae, the most species-rich genus being *Vittaria*. The last family of ferns with >30 epiphytic species is Davalliaceae with the two genera *Davallia* and *Davallodes*, which are entirely epiphytic.

Box 2.1 Epiphytes and Lithophytes

Lithophytes are defined as plants "that grow on rock and derive their nourishment chiefly from the atmosphere" (The American Heritage Science Dictionary 2005). The term was originally introduced by Schimper (1898), for both terrestrial and limnic/marine situations. A unifying characteristic is growth in extremely rocky situations with negligible humus. However, plants that grow on mossy riverside rocks (e.g., *Lepanthes rupestris*, Tremblay 1997) are also technically lithophytes, although their ecology may be primarily determined by disturbance and inundation by occasional floods rather than by drought and high temperatures. Thus, lithophytes and epiphytes share growth on a largely impenetrable substrate with resulting problems of anchorage and procurement of water and nutrients, and in both cases growing conditions can be increasingly similar to those of "normal" terrestrial plants.

Not surprisingly, a certain number of species are regularly found growing on both substrates, e.g., at least 1.3 % of all epiphytic *Epidendrum* (17 species), 2 % of all epiphytic *Aechmea* (4 species), and up to 5 % of all epiphytic *Vriesea* species (14 species) (WCSP 2014). These and other genera may also have a sizable proportion of truly lithophytic members. For example, the genus *Cattleya* with almost 100 truly epiphytic taxa counts with 14 species that are only found on rocks (13 % of all species) and another 4 species, which grow as both epiphytes and lithophytes, e.g., *Cattleya cernua* (WCSP 2014). Alves and Kolbek (2000) list about 20 species of herbs that are typically found on quartzite cliffs in Minas Gerais, Brazil. More than half of these so-called lithophytes grow usually, or at least very frequently, as epiphytes (e.g., *Aechmea nudicaulis, Cattleya cinnabarina*, or *Hatiora salicornioides*). The research opportunity to compare the performance of such facultative epiphyte/lithophytes in different habitats is largely unused (but see Gómez et al. 2006 or Xing et al. 2015).

The seeming resemblance of the growth conditions of a lithophyte and an epiphyte suggests that evolutionary transitions from lithophyte to epiphyte and vice versa may have been easier than those from the terrestrial habit to either of the two. However, it is unresolved how many transitions from terrestrial to epiphyte/lithophyte and vice versa were necessary to produce the patterns within the genera described above. Interesting links to lithophytic growth can also be assumed in the case of woody hemiepiphytes. Many researchers of the genus *Ficus* believe that the hemiepiphytic habit has evolved from lithophytic predecessors. There are many extant *Ficus* species growing as rocky shore plants and on cliffs. Arguably, this has led to the evolution of a propensity for long aerial roots and a certain tolerance to intermittent supply of water and nutrients, an important prerequisite for the evolution of full hemiepiphytism, which is so common in this genus (Zotz 2013).

(continued)

Box 2.1 (continued)

Overall, however, the percentage of typical epiphytes that also grow lithophytically on a regular basis seems to be rather limited, which suggests that the two habitats are far from identical in terms of the abiotic and biotic conditions. There are a number of immediately apparent differences. (1) In general, rocks represent a more stable substrate than the typical tree, (2) depending on rock type, roots may be able to penetrate to considerable depth with access to fine material (nutrients) and water, (3) and—compared to bark—fully exposed rock can reach much higher, and rather stressful, temperatures. For example, Arens and Pedraita (1948) measured 60.5 °C in 0.5 cm depth in a rock outcrop near Rio de Janeiro (air temperature was 35 °C). Although bark temperature can also substantially increase above air temperature during exposure to full solar radiation, I am not aware of any report of similarly high values for bark (compare Nicolai 1986; Schmid et al. 1991; Freiberg 2001).

The preceding list of differences between the epiphytic and lithophytic habitat is clearly incomplete, but may still be a starting point for interesting comparisons. It should be highly instructive to identify the mechanisms which allow or prevent growth of typical epiphytes on rocks and growth of lithophytes on trees.

Among the angiosperms, one family stands out, the Orchidaceae, which can best be expressed with the following statement: most epiphytes are orchids and most orchids are epiphytes! With almost 19,000 epiphytic species in 543 genera, Orchidaceae account for 68 % of all known epiphytes or 59 % of all genera with epiphytes. On the other hand, 69 % of all orchids (60 % of all orchid genera) are epiphytic. Among these are some of the most species-rich genera in the plant kingdom (Frodin 2004) such as *Bulbophyllum* (1866 species), *Dendrobium* (1448 species), and *Epidendrum* (1374 species). Interestingly, all have at least a few species that grow terrestrially or lithophytically (e.g., there are c. 30 non-epiphytic species of *Epidendrum*). In Kress (1986), all these genera were treated as exclusively epiphytic, which implied that the conquest of tree canopies had been unidirectional, constituting an evolutionary dead end. Table 2.1 shows that more than 50 basically epiphytic orchid genera have a few terrestrial and/or lithophytic members. This indicates a much more dynamic evolution of habitat preferences. The five subfamilies of Orchidaceae contribute very unevenly to these remarkable figures. Virtually all epiphytes are found in Epidendroideae, whereas fewer than 100 epiphytic species are known in all other subfamilies combined. The limited adaptation to the epiphytic lifestyle is also reflected by the fact that the few epiphytic members of these subfamilies are generally found in less challenging situations, e.g., in humus-filled crevices, bark fissures, or lichen-covered limbs in wet forests (Benzing and Atwood 1984).

Bromeliaceae is second in terms of numbers of epiphytic species among Magnoliidae with almost 1800 epiphyte species, which represent about 60 % of all family members. However, epiphytism is largely confined to the two subfamilies Tillandsioideae and Bromelioideae. With one exception (*Pitcairnia feliciana*, Jacques-Félix 2000), this family is only found in the New World, where its ecological importance, e.g., the contribution to total epiphyte biomass or the influence on canopy fauna, frequently exceeds that of orchids and all other groups of vascular epiphytes.

Peperomia (Piperaceae) is the genus with the largest numbers of epiphyte species apart from the orchid genera mentioned above. A revision of the approximately 1600 *Peperomia* species yielded about 700 epiphytes (M. Samain, pers. comm.). Another family with a substantial number of epiphyte species is Ericaceae. About 15 % of the c. 4000 species are epiphytic and c. 25 % of the genera in this family have at least one epiphytic member. In this family, the genus with the largest number of epiphytic species is *Rhododendron* (c. 140 epiphytic species) in the subfamily Ericoideae, while epiphytism is most common in the tribe Vaccinieae in the subfamily Vaccinioideae: 27 of c. 32 genera have at least a few epiphytic members. A large proportion of these species are not restricted to either the epiphytic or terrestrial existence. As observed by Luteyn (1989), Ericaceae have evolved the ability to exploit various habitats with numerous life forms even within a single genus. For example, most of the species in the genus *Cavendishia* are erect shrubs, which are often epiphytic, but there are also tiny pendent epiphytes (e.g., *Cavendishia barnebyi*), wiry or scandent subshrubs, or small trees. Slightly fewer epiphytic species (570 species) compared to the previous two families are found in Gesneriaceae. The two most important genera (total: 20 genera with epiphytes) are *Aeschynanthus* and *Columnea* with almost 200 species each. The distinction between vines, terrestrial herbs with accidental occurrences on trees, and epiphytes is frequently difficult. For example, most species of *Drymonia* germinate exclusively terrestrially, but there are a few species in this genus that can be classified as true epiphytes (e.g., Clark et al. 2006).

Aroids have traditionally been considered a family with one of the strongest epiphytic biases (Benzing 1990). Indeed, a large proportion of the estimated 3200 species use trees and other woody plants as structural support, but relatively few of them are true epiphytes. Most are nomadic vines in genera such as *Monstera, Syngonium*, or *Philodendron* (Holbrook and Putz 1996) with a completely different ecology. Excluding these species leads to a rather dramatic reduction, from c. 1300 "epiphytic" species counted by Kress (1986) to c. 230. Most belong to the genus *Anthurium* with c. 200 species of epiphytes. Many Cyclanthaceae are also vines, but about 50 species in genera such as *Sphaeradenia* or *Asplundia* grow regularly as epiphytes.

Most of the c. 4000 species of Melastomataceae are shrubs and herbs, while relatively few are at least facultatively epiphytic and hemiepiphytic species (c. 7 % or c. 300 species). Important genera with epiphytes/hemiepiphytes are *Blakea* and *Topobea* in the Neotropics and *Medinilla* in the Paleotropics. More than 20 genera of Rubiaceae have epiphytic members. Most species-rich and almost exclusively epiphytic are the genera *Hillia*, *Hydnophytum*, and *Myrmecodia*. Apocynaceae are mostly lianas, trees, and shrubs, but there are more than 100 species of obligate or at least facultative epiphytes, mostly in the two genera *Dischidia* and *Hoya*.

There are a similar number of epiphytic cacti in 15 genera. The most important genus of epiphytic Cactaceae is *Rhipsalis* with a center of diversity in the Atlantic rainforest of Brazil.

There are seven genera in the Solanaceae which are exclusively epiphytic or are (primary) hemiepiphytes, but none is particularly species-rich. A few taxa in the genera *Solanum* and *Lycianthes* are true epiphytes. Similar to many other cases, limits between epiphytes and terrestrials are not sharp: quite a few terrestrial species like the herbaceous vine, *Solanum phaseoloides*, occasionally grow either on fallen logs or as an epiphyte (Tepe and Bohs 2011).

Most of the species listed in Table 2.1 in the four families Clusiaceae, Urticaceae, Moraceae, and Araliaceae are not true epiphytes, but (facultative) hemiepiphytes. In Moraceae, all *Ficus* species in the subgenera *Urostigma* and *Sycidium* are (potentially) hemiepiphytic, although some may primarily grow as lithophytes or banyans. Interestingly, the only truly epiphytic *Ficus* species, *Ficus deltoidea* var. *borneensis* Corner (R. Harrison, pers. comm.), belongs to the subgenus *Ficus*, a group basically composed of shrubs and trees. Most included taxa of the family Araliaceae are basically trees, shrubs, or lianas, which use other trees only facultatively as substrate for establishment. Lack of quantitative information renders the distinction between facultative and accidental (hemi)epiphyte currently impossible. By far the most important genus in this family is *Schefflera* with at least 42 species that regularly grow epiphytically. Hemiepiphytes are also found in many other families; e.g., the genus *Fagraea* (Gentianaceae) offers a wide range of life forms from trees, shrub, and lianas to true epiphytes and hemiepiphytes, often with substantial variation within a single species.

Asteraceae, Begoniaceae, and Zingiberaceae are basically terrestrial plant families, with a moderate number of epiphytic species (36–49) per family, but a similar number of epiphytic taxa (34) in monogeneric Nepenthaceae indicates a substantial epiphytic bias: about one-third of the 104 species of *Nepenthes* are epiphytic.

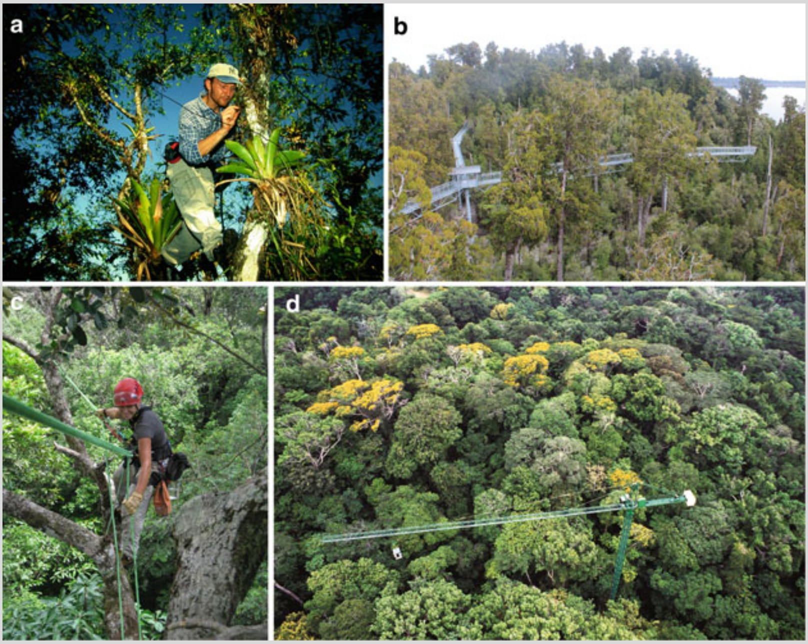
2.1.2 Future Changes in the Proportion of Epiphytic Taxa

Clearly, all the figures in the previous paragraphs depend upon, often debated, species delimitations and on the used definition of "epiphyte." An example for a contentious case is the inclusion of two hemiparasitic taxa, *Gaiadendron punctatum* (Kuijt 1963) and *Pedicularis dendrothauma* (Allard et al. 2005). In contrast to the typical mistletoe, both typically parasitize other epiphytes and not the host tree. Hence, their inclusion depends upon the interpretation of the "nonparasitic" in our definition of an epiphyte—does this attribute refer only to the interaction with the host or to that with any plant? Even ignoring such potential sources of dispute, the numbers of epiphyte species are bound to change because new species continue to be described, and presently accepted taxa may be revised. Currently, there are about 290,000 described species of vascular plants, but estimates for flowering plants assume that continuing exploration will raise that number by about 10–20 % (Joppa et al. 2010). Will the final proportion of vascular epiphytes still remain close to the current 9 % (Zotz 2013)? Tree canopies have been repeatedly called the "last" or "final" biotic frontier (Erwin 1988; Wilson 1992). Considering that epiphytes live in this habitat, the increased access of researchers to the upper strata of forests, particularly in the tropics (Box 2.2), should have led to a relatively larger proportion of epiphytic taxa in the last decades, if access problems were indeed responsible for biased estimates in favor of soil-rooted plants. Surprisingly, an analysis of the proportion of epiphytic taxa among newly described orchid and bromeliad species over more than 200 years using the WCSP database (WCSP 2014) seems to indicate otherwise. The decadal average of the proportion of epiphytic orchids among newly described taxa has been nearly constant 66 % since 1830 ($p = 0.3$, Pearson Product-Moment correlation, Zotz 2013). Only the species described before 1830 had a much lower proportion of epiphytes, c. 25 %. A similar result is found for Bromeliaceae: the proportion of epiphytic taxa during 25-year intervals has not changed since 1750 ($p = 0.1$, Pearson Product-Moment correlation). There is no reason to believe that other families with a large proportion of epiphytic members deviate from this pattern, and, hence, it seems unlikely that the grand picture of the distribution of epiphytes among vascular plants will undergo any major change during future revisions. Continued discoveries of epiphytic taxa in smaller families are a different issue. For example, compared to Kress (1986), the number of epiphytic *Impatiens* (Balsaminaceae) has tripled (from 5 to 15 species) (e.g., Janssens et al. 2010) and the number of epiphytic Crassulaceae even quadrupled to some 20 species (Eggli 2003). Finally, the number of known epiphytic *Nepenthes* has even risen by 500 % from 6 to 34 species (McPherson 2009). Revisions of the most recent list will also be necessary as improved natural history information becomes available or as omissions become apparent. An example for the former is Marcgraviaceae. Previous compilations had treated most species of this family as nomadic vines, which caused their exclusion by Zotz (2013). However, evidence from several sources (e.g., an unpublished MSc thesis (Massa 1996) and pers. comm. from Nils Köster, Berlin) indicates that at least some members of this family, e.g., *Marcgravia brownie* in Ecuador, germinate mostly epiphytically and thus qualify as epiphytes or at least as hemiepiphytes. Thus, future revisions of the list of epiphytic plants should include this family again (Table 2.1). Other omissions in Zotz (2013) are Pandanaceae—there are at least five known epiphytic pandan species of the genus *Benstonea* (Callmander et al. 2013, and Callmander, pers. comm.) and Liliaceae - there are two epiphytic species (Shaw 2008). This increases the number of known families with epiphytes to 76. To conclude, although the basic pattern is settled, there is still substantial and continuous need for corrections and updates.

Box 2.2 Canopy Access

Canopy access has always been a challenge, unless researchers restricted themselves to the study of lower epiphytes (<2 m above the ground), which can be observed directly or, if attached somewhat higher on a tree, are accessible with, e.g., a ladder. One rather drastic option, which allowed the close-up observation of epiphytes in the upper parts of taller trees, was felling the tree as done in the classic study on epiphyte ecology by Johansson (1974). Today there are many alternatives for nondestructive and repeated access.

The following pictures illustrate different canopy access methods currently in use: (A) free climbing (Gerold Schmidt, Barro Colorado, Panama), (B) canopy walkway (Hokitika, New Zealand), (C) single or double rope climbing (Valentine Alt, Nourague, French Guyana), (D) canopy crane (San Lorenzo, Panama). (Photographs a: Christian Ziegler, c: Helena Einzmann, d: Smithsonian Tropical Research Institute).



2.2 The Conquest of Tree Canopies: "Up" and Sometimes "Down"

The fossil record for vascular epiphytes is poor. Moreover, the interpretation of described fossils is subject to debate, since the unequivocal association of, e.g., the carboniferous ferns *Botryopteris forensis* (Rothwell 1991) or *Tubicaulis scandens* (Mamay 1952) with the trunks of tree ferns can either be taken as evidence for their epiphytic existence as early as 300–350 million years ago or, alternatively, be explained as growth on a fallen trunk as observed in many extant terrestrial ferns (DiMichelle and Phillips 2002; Watkins and Cardelus 2012). There is one possible exception: Psenicka and Oplustil (2013) recently described two fossilized *Selaginella* species in in situ volcanic ash-fall deposits from the Pennsylvanian (c. 310 Million years ago). Specimens were attached to arborescent gymnosperms (*Cordaites*) or lycopsids (*Lepidodendron*) and were found 30–60 cm above the tuff bed base. Currently, this is the best evidence for the paleozoic existence of vascular epiphytes. In contrast, more abundant and less ambiguous fossil evidence for epiphytic growth is available from the Cenozoic, e.g., for orchids (Conran et al. 2009), aroids (Herrera et al. 2008), or ferns (Poole and Page 2000; Su et al. 2011). There are two possible explanations for this situation. Either epiphytes have a very low potential for fossilization or the epiphytic life form was simply rare before the advent of modern ecosystems. The disproportionate contribution of geologically older ferns and lycopods to extant epiphytic flora (Sect. 2.1) has been used as an argument for the first notion, but there is actually increasing evidence supporting the second notion.

Current global vegetation is dominated by angiosperms, which appeared during the early Cretaceous, but their dominance was probably not complete before the late Cretaceous (Beerling and Woodward 1997; Ziegler et al. 2003; Davis et al. 2005). Molecular studies provide convincing evidence for an explosive radiation of epiphytic fern lineages “in the shadow of angiosperms” (Schneider et al. 2004). Almost all diversification among extant epiphytic ferns (Schuettpelz and Pryer 2009) and lycopods (Wikström et al. 1999) occurred during the late Cretaceous and the early Tertiary (K/T boundary). What were the reasons for this explosive radiation? For one, the replacement of dominant gymnosperms by angiosperms may have directly promoted epiphytic growth. Most extant gymnosperms seem to be much poorer hosts for epiphytes than the majority of angiosperm trees (Sect. 7.2, Watkins and Cardelus 2012; Zotz 2005; but compare, e.g., New Zealand Podocarps: Dawson and Sneddon 1969) possibly due to their bark characteristics and their crown architecture. Similarly important, the climate at the K/T boundary allowed the development of “modern” rainforests. Arguably, a combination of increased tree structural complexity and tropical climate boosted the conquest and subsequent radiation in tree crowns by ferns and nonwoody angiosperm lineages such as Orchidaceae, the most important contributor to current epiphyte diversity (Ramirez et al. 2007).

Epiphytism appears to foster speciation within lineages (Gravendeel et al. 2004; but see Sundue et al. 2015 for a contrasting finding), which seems to be true for other structurally dependent plant groups such as climbing plants (Gianoli 2004) or nonvascular epiphytes (Shaw et al. 2003) as well. Gravendeel et al. (2004) found significantly higher species numbers in epiphytic genera compared to terrestrial ones, both for orchids and non-orchids. Similarly, 12 of the 57 *big* plant genera in the Magnoliidae (sensu Frodin 2004, genera with >500 species) are almost entirely epiphytic (e.g., *Bulbophyllum*, *Epidendrum*) or have a strong epiphytic bias (e.g., *Peperomia*, *Rhododendron*). The exact mechanism(s) behind this enormous diversity remain obscure. Phillips et al. (2012) tested an hypothesis put forward specifically for orchids by Gentry and Dodson (1987): small, disjunct orchid populations experience strong genetic drift, e.g., due to orogenesis, which then promotes the formation of new species. However, their meta-analysis of 52 allozyme studies yielded no evidence for high levels of population genetic differentiation. To date, there is thus no entirely convincing explanation for the enormous diversity in orchids and any other species-rich epiphyte group.

Starting an epiphytic existence is not a unidirectional evolutionary process. There are a number of examples for the opposite path. A good example is *Huperzia s.l.*, a genus with c. 300 terrestrial and epiphytic species. The c. 200 tree-dwelling species of this genus apparently represent a single switch from the plesiomorphic terrestrial state before the final rifting of South America and Africa, followed by at least two subsequent reversals to the terrestrial habit (Wikström et al. 1999). Molecular phylogenies suggest that terrestrial *Huperzia* species in the high Andes are not derived from terrestrial ancestors from the temperate zone as previously assumed, but from epiphytic species from montane regions in the New World. An even more elaborate analysis of the evolution of the epiphytic habit in this genus has appeared very recently (Field et al. 2016). Similar scenarios seem to apply for many other genera of ferns and angiosperms: not fewer than 50 basically epiphytic genera of orchids have some terrestrial and/or lithophytic members (Monteiro et al. 2010; Zotz 2013).

Are there evolutionary connections of true epiphytes with other structurally dependent plants, i.e., climbing plants (lianas, nomadic vines, hemiepiphytes, Fig. 1.3)? The families with major proportions of vascular epiphytes (e.g., orchids, bromeliads) have no or very few climbing taxa and no hemiepiphytes. Thus, the vast majority of current epiphytes can probably be linked to direct colonization events from terrestrial ancestors and later radiations in tree crowns. Accidental epiphytes in these and other families may be seen as species currently performing "evolutionary trials" to conquer tree crowns and certainly deserve much more attention—since accidental epiphytes usually constitute a nonrandom sample of local floras (Zotz and List 2003), a trait analysis should reveal interesting patterns. However, there is little doubt that epiphytism has also evolved via intermediate steps. Tsutsumi and Kato (2006) suggest, for example, that obligate epiphytes in Davalliaceae and polygrammoid ferns evolved from nomadic vines, which in turn developed from true climbers. On the other hand, the discovery of (primary) hemiepiphytism in *Elaphoglossum amygdalifolium*, a basal species within that fern genus, prompted Lagomarsino et al. (2012) to suggest that hemiepiphytism was the intermediate step between the climbing habit in other bolbitidoid genera and the true epiphytism found in the majority of *Elaphoglossum* species. Others consider hemiepiphytism an evolutionary pathway that is independent of the transition from terrestrial to epiphytic growth in other fern taxa (Dubuisson et al. 2003). Another example for transitions concerns woody hemiepiphytes: some individuals of usually hemiepiphytic *Griselinia lucida* (Bryan et al. 2011) reproduce during their epiphytic stage (C. Kirby, pers. comm.) and would thus "qualify" as true epiphytes. All these scenarios are not mutually exclusive and may simply reflect alternative trajectories in different lineages. The aroids, in particular, constitute a largely unused research opportunity in this regard. There are epiphytes, vines, nomadic vines, and hemiepiphytes in closely related taxa (Croat 1988), with variation even within species (Zotz 2004).

2.3 How Biased Is Our Current View on Epiphytes?

Does research on the biology of vascular epiphytes reflect their actual diversity, in regard to taxonomy and differences in geographical distributions? This is clearly not the case. For one, there is a substantial taxonomic bias as revealed by a bibliometric analysis of the numbers of publications on the biology of vascular epiphytes. In absolute number, three groups (Orchidaceae, Bromeliaceae, and "ferns") have received far more attention than other important families (Fig. 2.4), but relative to their species numbers, cacti stand out. There are about twice as many publications per species on epiphytic Cactaceae than on Bromeliaceae and 20 times more than on Orchidaceae. The latter family, by far the largest contributor to epiphyte species diversity, is extremely understudied relative to species numbers: our understanding of orchid ecology is arguably very superficial.

Information on vascular epiphytes is not only highly biased taxonomically, but also geographically, which I quantified with another bibliometric analysis of 2753 ecological articles (Fig. 2.5) from the primary literature (journal articles, reports, and non-review chapters in conference proceedings), covering a time span from the late nineteenth century with classics such as Schimper (1888) up to the recent publications from August 2015. Ecology was defined in the widest possible sense, including species lists, local inventories, (eco)physiological studies, morphological-anatomical, yet not purely taxonomic, studies to those on the interactions with animals, on ethnobotany, or papers with a conservation context.

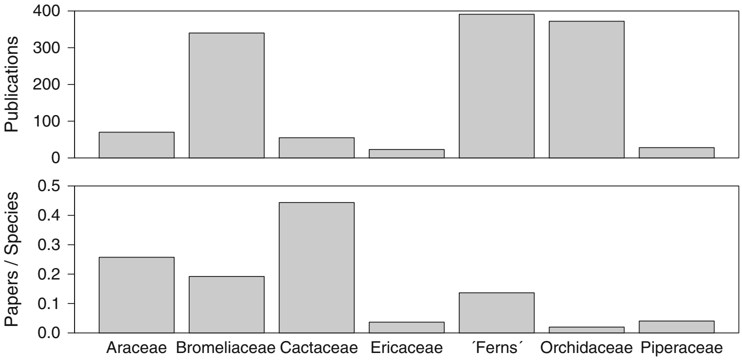


Fig. 2.4 Bibliometric analysis of research effort and number of epiphytic taxa in different plant groups. Shown are the results of the search ("epiphyt* and 'taxon name'") in the Web of Science® database in October 2015. The ratio of paper/species was calculated using the numbers per group from Zotz (2013)

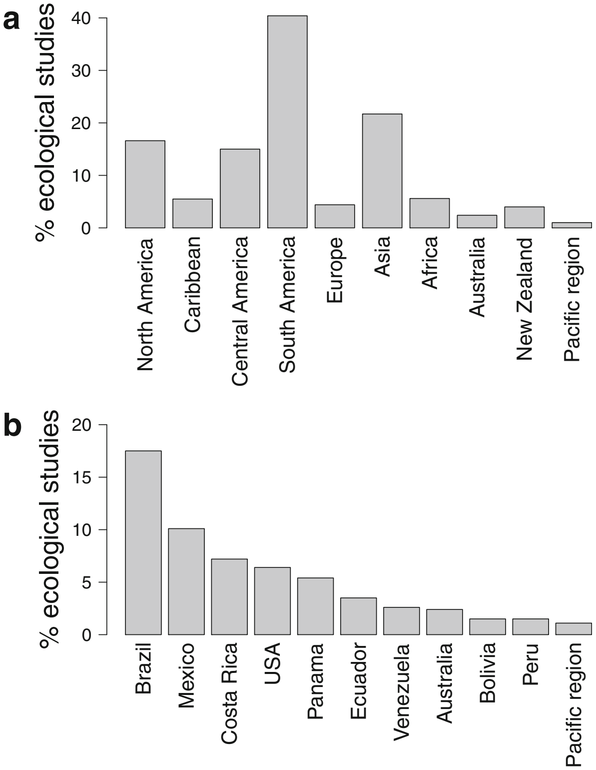


Fig. 2.5 Geographic bias in the publications on epiphytes. Based on a collection of 2753 scholarly papers, theses, and book chapters published since 1888. Descriptive and experimental studies covering ecological topics in the widest sense were included, e.g., work on demography, functional ecology, functional anatomy, or species inventories, even when the main focus was not on epiphytes themselves, e.g., biodiversity studies in phytotelmata or reports of bird foraging in epiphytes. Purely taxonomic or horticultural papers were not considered. The contribution to the literature is specified by major regions/continents (*upper panel*) and countries (*lower panel*)

More than 77 % of these *ecological* studies are from the Americas, which in part reflects the high epiphyte richness of the Neotropics (Chap. 3). Remarkably, there are more publications from north-temperate Europe with just a few facultatively epiphytic ferns (e.g., *Polypodium vulgare*, *Hymenophyllum peltatum, H. tunbrigense*) than from epiphyte-rich New Zealand in the Southern hemisphere. Not surprisingly, most studies in Europe focused on accidental and facultative epiphytes. An even more remarkable geographic bias becomes apparent when comparing the temperate USA with tropical Ecuador. There are about twice the number of publications on vascular epiphytes from the USA, with 85 native epiphytic ferns and flowering plants, compared to hyperdiverse Ecuador, which is estimated to be home to about 50 times this number with about 4300 species of vascular epiphytes (Küper et al. 2004). The high impact of successful field stations is apparent when comparing individual countries. Although Brazil is the country with the highest absolute number of publications on epiphytes, this number is dwarfed when compared with tiny Costa Rica with famous research stations in La Selva or Monteverde: on an area-basis scientific output from Costa Rica is almost two orders of magnitude higher.

I urge the reader to keep these taxonomic and geographic biases in mind. Throughout this monograph, any generalization should be treated with caution and future work should try to achieve a more balanced taxonomic and geographic representation.

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3 Biogeography: Latitudinal and Elevational Trends

The global, continental, and regional distribution of vascular epiphytes shows a number of particularities compared to other plant life forms. Generally, distributional ranges of epiphytes tend to be broader than those of closely related terrestrial and lithophytic species (Ibisch et al. 1996; Kessler 2002a). This is linked—at least in part—to a high capacity for long-distance dispersal among epiphytes (Kessler 2002a). However, other factors affect epiphyte distribution as well. They are generally more closely coupled to the atmospheric humidity than most other life forms, e.g., soil-rooted herbaceous plants. This should make epiphytes more prone to suffer from drought and frost, differentially affecting both their latitudinal and elevational distributions.

We are currently in the process of analyzing the global distribution of vascular epiphytes. It will still take a considerable amount of time until the geographical information for the c. 28,000 known taxa will be compiled and analyzed. In this chapter, I can at least present preliminary global diversity maps of two of the most important groups: the orchids and the ferns and fern allies, which are based on the most recent distributional data (Fig. 3.1).

3.1 Latitudinal Trends

Latitudinal diversity gradients with maxima in the tropics are typical for most groups of organisms (Willig 2003), but the association of vascular epiphytes with the wet tropics seems to be particularly tight. Some authors even explicitly include epiphytes as defining features of tropical rainforests (e.g., Richards 1996) or tropical montane cloud forests (Grubb et al. 1963). However, vascular epiphytes

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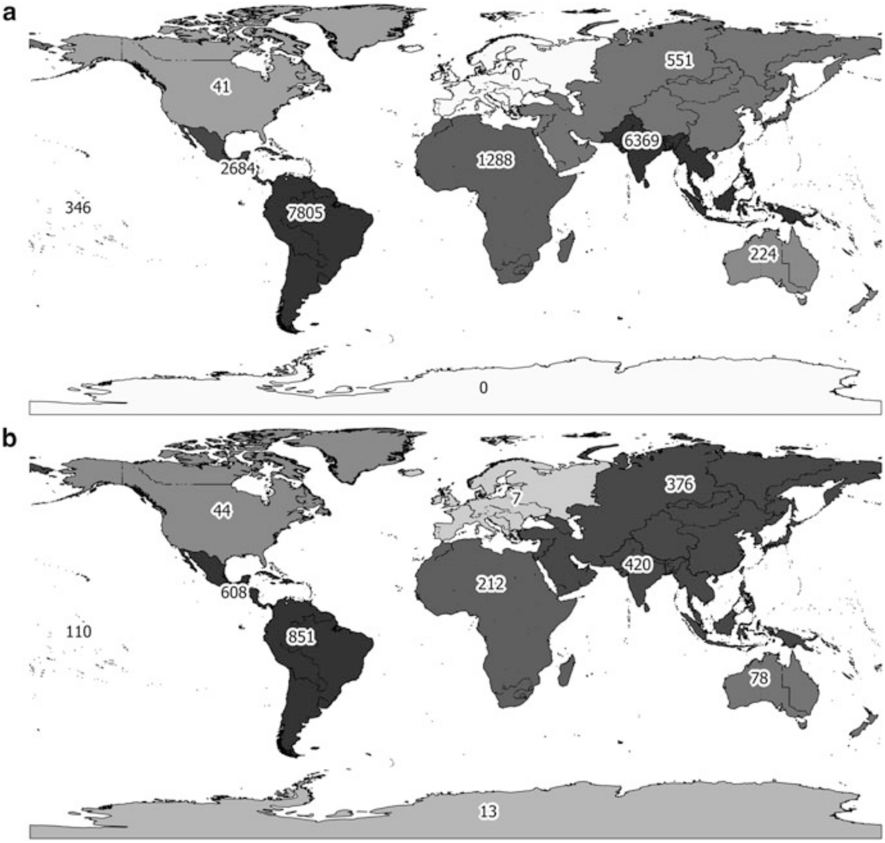


Fig. 3.1 Global distribution of orchids and ferns/fern allies. The number of epiphytic species is summed up for major geographical regions (North America, Mesoamerica/Caribbean, South America, Africa, Europe, Northern Asia, Southern Asia, Australia/New Zealand, Pacific Region, Antarctica/subantarctic islands). Increasingly *dark* hues of *gray* indicate higher species numbers. Geographic data for orchids (**a**) from WCSP and other sources; data for ferns (**b**) from Hassler and Schmitt (2015) and other sources. Maps produced by Laura Kuijpers

can be quite diverse and/or abundant in extratropical vegetation (Box 3.1). For example, Oliver (1930) listed 50 species of "typical" epiphytes, corresponding to c. 2 % of the native flora of New Zealand, and within the "Valdivian rainforests" of Chile epiphytes account for c. 10 % of all vascular plants (Arroyo et al. 1995), while Sillett and Bailey (2003) report a stunning 740 kg of epiphytic matter of *Polypodium scouleri* mats in a single redwood tree in California, USA.

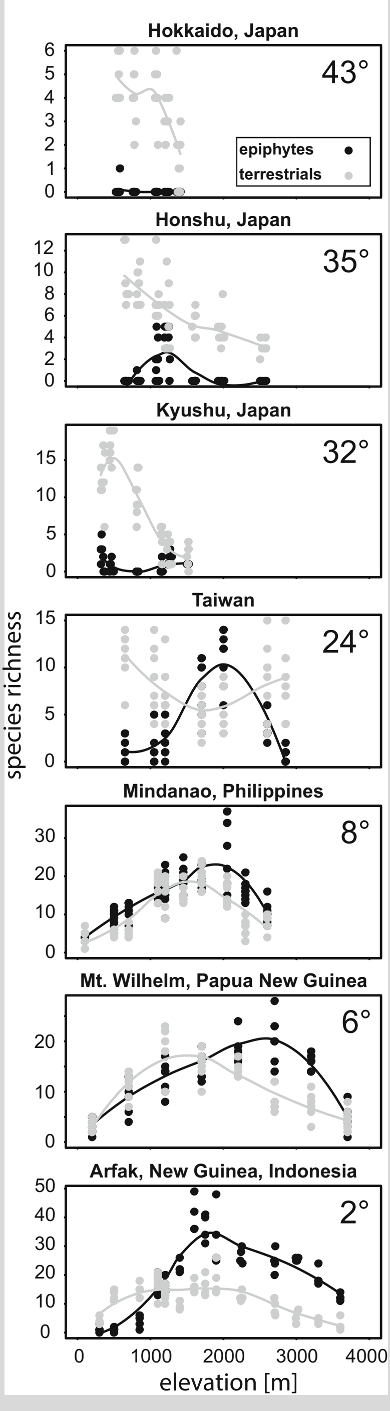
Box 3.1 Comparing Species Richness Patterns of Epiphytic and Terrestrial Ferns Along Elevational and Latitudinal Gradients (Dirk Nikolaus Karger, Jürgen Kluge, and Michael Kessler)

Epiphytes often show strikingly different patterns of species richness along elevational and latitudinal gradients when compared to terrestrial species (Kessler 2001a, b). These different patterns can be well observed in the ferns, a globally distributed plant group with high numbers of epiphytic and terrestrial species. Investigating several elevational gradients ranging from the tropics to the temperate zones in the Asian Pacific region, it becomes apparent that terrestrial richness is by far higher than epiphytic richness in the temperate zones, whereas in the tropics the opposite is true.

The figure below shows species richness patterns of epiphytic (black dots and lines) and terrestrial (gray dots and lines) ferns along seven elevational gradients in the Asian Pacific region. Species richness represents the number of species encountered in standardized survey plots of $20 \times 20\ \mathrm{m}^2$ within forests. (Trendlines were fitted using locally weighted regression.). In the tropics, the areas with the highest epiphytic richness are found at mid elevations, between 2000 and 3000 m. Towards higher latitudes, epiphytic richness declines sharply, and the maximum richness shifts toward lower elevations. Similar shifts of richness patterns are apparent for terrestrial species, but neither does terrestrial fern richness decline as fast with elevation, nor latitude, as it does for epiphytic species. While the overall patterns of fern species richness along both gradients are generally considered to be driven by climatic factors (Kessler et al. 2011b), area (Karger et al. 2011), dispersal processes (Kessler et al. 2011a), or geometric constraints (Kluge et al. 2006), the difference between terrestrial and epiphytic patterns has not been investigated in depth for ferns, nor any other plant group, for that matter. We consider the following potential explanations. (1) Microclimatic conditions may be harsher in the canopy habitat, so that even though the physiological tolerances of epiphytes are similar to those of terrestrials, they may reach their distributional limits under more favorable macroclimatic conditions. (2) Alternatively, epiphytic plants may be physiologically more restricted than terrestrial ones, because adaptations to some factors in the epiphytic realm (e.g., low water availability) may constrain their physiological tolerances to other factors (e.g., low temperatures). (3) The epiphytic habitat was evolutionarily explored later than the terrestrial one (Schneider et al. 2004) so that epiphytes have not yet evolved their full potential niche volume.

(continued)

Box 3.1 (continued)



Among nontropical regions, there is a pronounced hemispherical asymmetry in the latitudinal trend from the tropics toward the poles, which was first noted by Schimper (1888) and has been discussed in detail by Zotz (2003, 2005). For example, there are just two species of epiphytes in Caverns State Park in the USA (30° N), while there are 15 such species in Puyehue National Park in Chile (41° S) (Gentry and Dodson 1987). The most diverse region in respect to vascular epiphytes in the north-temperate zone are the Himalayas, but locally abundant epiphyte populations are also documented for temperate East Asia, the Caucasus, in montane forests in Central Europe, the British Isles, several Atlantic islands, and northwest North America (Zotz 2005). Most taxa in typical epiphyte floras in the temperate zones have tropical affinities (e.g., *Earina* spp. in New Zealand or *Epidendrum* spp. in the USA), but there are at least a few temperate elements, e.g., the monotypic fern genus *Synammia* in Chile.

Apart from varying diversity, taxonomic participation also differs substantially between tropical and temperate epiphytes floras. The former are usually dominated by orchids, while the latter have a very high proportion of ferns and fern allies, which often belong to the genus *Polypodium* (Table 3.1, Fig. 3.1). A large percentage of accidental epiphytes represent another difference to epiphyte communities in the tropics. While rather exceptional there (compare, e.g., Zotz et al. 1999; Nieder et al. 2000; Zotz and Schultz 2008), almost 75 % of all species growing epiphytically in a *Nothofagus* forest in New Zealand were accidental epiphytes (Hofstede et al. 2001). An even higher proportion of accidental epiphytes, c. 90 %, were found in a temperate rainforest in British Columbia (Burns 2008). It may be more enlightening to interpret this latitudinal difference as a relative rarity in the tropics rather than a relative commonness in the temperate zones. The impression of rarity of accidental epiphytes in the tropics is based on relatively few data, so future work has to show its generality. Assuming this to be the case we could start to investigate the underlying mechanism. Given that many epiphyte assemblages are not saturated (Chap. 7) competitive exclusion by established epiphytes cannot serve as an obvious explanation (but see Nadkarni and Solano 2002). Investigating this puzzle may provide some important insights into the biology of epiphytes.

Table 3.1 Proportion of major taxonomic groups among vascular epiphyte species in moist and wet tropical forests and temperate forests

Taxonomic group/Species numbers (%)	Tropical forests	Temperate forests
Total species number in census area	164 ± 102	20 ± 17
Orchidaceae (%)	48 ± 10	9 ± 11
Ferns and fern allies (%)	24 ± 6	77 ± 16
Bromeliaceae (%)	7 ± 5	2 ± 4
Araceae (%)	6 ± 6	0
Piperaceae (%)	4 ± 2	0.3 ± 1.1
Ericaceae (%)	2 ± 3	0.1 ± 0.6

Data are based on 16 studies in the tropics and 14 studies in the temperate zones. Given are total species numbers and percentages (average ± SD for each group). Condensed from Zotz (2005)

All temperate regions with a rich epiphyte flora (i.e., New Zealand, Chile, Himalayas, Japan) are characterized by humid climates with few incidences of frost (Zotz 2005). This observation has prompted two principal explanations for the observed biogeographic pattern. Schimper (1888) stressed low water availability in the temperate zones, whereas others (e.g., Benzing 1990 or Nieder and Barthlott 2001) emphasized the impact of frost. Epiphytes comprise a very diverse group, both taxonomically and ecologically, and it seems unlikely that there is a single, universal mechanism underlying their global distribution. For example, "tropical" families such as Araceae are probably mostly limited by low temperature in extratropical regions (Mayo et al. 1997), but this argument does not apply to the cosmopolitan ferns and fern allies, characterized by substantial freezing tolerance when growing as terrestrials (Kappen 1964). In addition, there are other possible explanations, e.g., the possibility that Pleistocene extinctions have led to a currently underexploited "epiphytic niche" due to a migrational lag (compare Normand et al. 2011 for a general treatment of postglacial), biotic interactions with potential host trees, and/or biogeographic considerations, e.g., the effect of distance to potential (tropical) source areas (compare, e.g., the depauperate epiphyte flora of western Europe with that of the Himalayas or the Southern USA).

Arguably, low moisture availability limits the development of epiphytism more than any other environmental factor in the temperate zones, similar to the tropics (Gentry and Dodson 1987). However, even in the driest tropical forests there are generally at least some epiphytes (Murphy and Lugo 1986); some species like the atmospheric bromeliad *Tillandsia recurvata* may be found in Interandean dry valleys (Fig. 3.2) and even in deserts as long as there is regular moisture input from mist (MacMahon and Wagner 1985). Many moist temperate forests, on the other hand, harbor no or only very few epiphytes, while the parts of the Himalayas with several months of drought may host a rich epiphyte flora. Thus, moisture availability alone cannot explain the latitudinal trend.

Low temperatures, let alone long-lasting frost, are likely to constitute a major limiting factor for most tropical taxa (Benzing 1990; Larson 1992). Garth (1964), however, suggested that temperature itself is not determining the northern limit of *Tillandsia usneoides* in North America, although a more recent study suggests otherwise (Barve et al. 2014). The only other temperate species studied in this respect is *Polypodium vulgare* (Kappen 1964; see Sect. 5.3). Similar to seasonally low temperatures in the temperate zones, recurring nocturnal frost in upper montane areas in the tropics may be the reason for the upper *elevational* limits of vascular epiphytes (Kessler 2002b). In summary, low temperatures are likely to act as a major filter for many of the tropical (lowland) epiphyte taxa, but we still lack quantitative evidence. Studies on the frost tolerance of epiphytes from the temperate zones and upper montane areas in the tropics are needed.

Differences in Pleistocene history between hemispheres are a potentially important aspect, but are rarely referred to as an explanation of current global distributions. Temperate regions with a high number of extant epiphyte species (i.e., Chile, New Zealand, Himalayas, Japan) have all been affected rather little by Pleistocene glaciations and/or provided refugia allowing the survival of tertiary

Fig. 3.2 Epiphytes in an Interandean dry valley. The columnar cacti are almost completely covered with epiphytic *Tillandsia* sp. in northern Peru

vegetation (e.g., Arroyo et al. 1995; Dawson 1986). Similar to terrestrial plants, temperate epiphyte communities are possibly far from saturated floristically, especially in Europe with its much poorer flora compared to North America or temperate East Asia. Unfortunately, direct evidence for possible changes in the epiphyte floras is very limited due to the poor fossil record of vascular epiphytes (Sect. 2.2, Collinson 2000). While regions with Pleistocene refugia (e.g., in Chile, New Zealand) feature many autochthonous taxa, the "epiphytic niche" in other areas (e.g., Southeast United States) was probably refilled in the Holocene by plants from lower latitudes and less by locally evolved members with the epiphytic habit (e.g., species of the *Polypodium vulgare* complex in Europe or North America). This scenario emphasizes the influence of history and geographical proximity to possible source areas in creating the current global patterns of plant species distributions (Ricklefs et al. 1999).

Finally, the possible role of host plant identity should not be ignored. It has been observed repeatedly that many conifers are poor hosts for epiphytes (Fig. 10.6, Zotz and List 2003; Garth 1964; Kramer 1993; Bir 1989; Carvajal-Hernández et al. 2014). There are a number of possible reasons, which are, e.g., related to bark chemistry or tree architecture. There are possible direct allelopathic effects or indirect ones; e.g., conifers with dense foliage may intercept a much higher proportion of rainfall and feature significantly reduced stemflow compared to deciduous angiosperms, leading to considerably lower water supply to epiphytes (Sect. 7.2, Watkins and Cardelus 2012).

3.2 Elevational Trends

Results from single-site studies had long suggested that epiphyte abundance and diversity is highest in cloud forests at intermediate elevations (e.g., Gentry and Dodson 1987). Epiphytes are not exceptional in this regard: a large number of studies, which were last reviewed by Rahbek (2005) and included a wide variety of organisms, clearly demonstrate that hump-shaped richness patterns are far more common (c. 50 %) than other patterns, in particular monotonic declines (c. 25 %). Some studies focused specifically on richness patterns in vascular epiphytes over large elevational gradients (Cardelús et al. 2006: 30–2600 m a.s.l.; Krömer et al. 2005: 350–4000 m a.s.l.), others over similarly large gradients included epiphytes and other life forms and analyzed them separately (e.g., Zhang et al. 2015; Watkins et al. 2006; Acharya et al. 2011). The results of these studies invariably identified a typical mid-elevation bulge (Fig. 3.3), although particular groups such as aroids differed and showed a monotonic decline. While this elevational pattern as such is rather well established for epiphytes in general (Box 3.1), the underlying causes are debated as for most other organisms. Climatic factors, mostly water availability, are typically the best predictors of this pattern, while other mechanisms, e.g., geographic constraints (the "mid-domain effect," Currie and Kerr 2008; Zhang et al. 2015), seem to play a minor role.

Irrespective of total species richness, there are changes in the composition of the epiphyte flora with elevation. Whereas aroids and orchids typically contribute substantially to the species pool in the lowlands and mid-elevations, respectively, ferns often dominate at the highest elevations, which mirrors the increasing

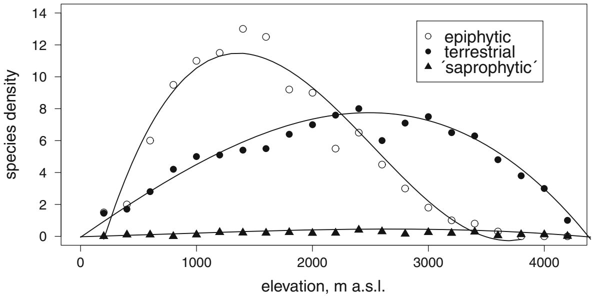


Fig. 3.3 Relationship of species density in Orchidaceae and elevation in Yunnan, China. Three life forms are distinguished, namely, epiphytes, autotrophic terrestrials, and "saprophytes" (=myco-heterotrophs). Modified after Zhang et al. (2015)

Fig. 3.4 (**a**) *Polylepis pepei* stand in the Cordillera Vilcabamba Southern Peru. This is the record elevation (4550 m asl) for any vascular epiphyte reported so far (Sylvester et al. 2014). (**b**) A close-up of *Melpomene peruviana*, Polypodiaceae (Photographs: Steven Sylvester)

importance of this group in epiphytic floras along the *latitudinal* gradient (Table 3.1). For example, Johansson (1974) reports that epiphytes on trees near the forest boundary on Mount Kenya (at approximately 3200 m a.s.l.) are all ferns, e.g., *Asplenium* and *Pleopeltis* species, while epiphytic orchids, which are common at the lower elevations, are entirely missing. Epiphytes at even higher elevations (>4000 m a.s.l.) in *Polylepis* stands in the Peruvian Andes are also exclusively polypodioid ferns (Fig. 3.4, Sylvester et al. 2014). On the other hand, epiphytic orchids and Ericaceae are almost as species-rich and abundant as ferns in subalpine elfin forest in Ecuador, and epiphytic orchids (e.g., *Beclardia macrostachya*) can be found in low-statured Páramo vegetation (c. 2800 m a.s.l., Bussmann 2003). Similarly, a recent study in Panama in *Comarostaphylis arbutoides* stands near the tree line at the summit of Volcán Barú (c. 3300 m, Zotz et al. 2014) documented sizeable populations of several epiphytic orchids. Even outside the tropics, e.g., in the Western Himalayas, epiphytic orchids such as *Dendrobium moniliforme* or *Pleione* spp. may be found at elevations up to 3000 m a.s.l. (Jalal and Jayanthi 2015). What limits the uppermost occurrence of particular taxa remains unclear. Possibly it is the absence of trees itself, although this notion is not entirely compatible with Bussmann's (2003) observations in Páramo vegetation, where shrubs offer substrate for colonization, or where usually epiphytic taxa switch to terrestrial growth. Ibisch et al. (2000) discussed this issue for epiphytic cacti in Bolivia. Although frost had been proposed as causal for the absence of epiphytic cacti above 2500 m a.s.l., the occurrence of taxa like *Rhipsalis baccifera* in regions with regular frost argues against temperature as the sole factor (see also Sect. 5.3).

3.3 Diversity Patterns Within the Tropics

It is well established that epiphytes respond more strongly to moisture availability with changes in abundance and diversity than other life forms (Gentry and Dodson 1987). This alone may explain the latitudinal and elevational patterns described

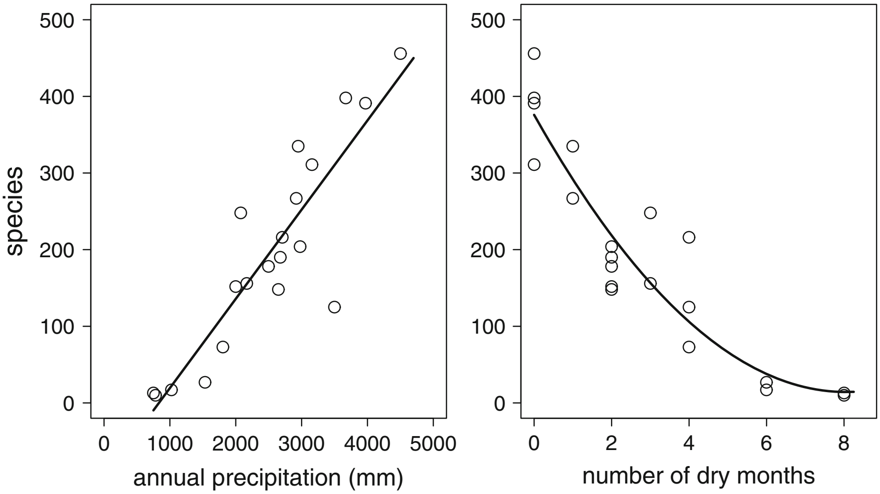


Fig. 3.5 Relationships of epiphyte species richness and mean annual precipitation, respectively, and the length of dry season (<100 mm of rain) at various Neotropical lowland sites. Details for the sites and references of individual studies can be found in Kreft et al. (2004), Wester et al. (2011), and Cuevas-Reyes and Vega-Gutiérrez (2012). *Solid lines* are regressions (r^2 values 0.77 and 0.86, $p < 0.05$)

above to a considerable extent and may also partly explain intercontinental differences (see below). It is also of major importance for the persistence of epiphyte assemblages when land-use changes (e.g., selective logging) lead to long-lasting microenvironmental changes (Chap. 10). The analysis of 19 epiphyte inventories in Neotropical lowland sites with diverse vegetation, ranging from dry forests to perhumid forests, gives a very clear message (Fig. 3.5): species richness is a tight function of moisture availability, whether expressed as mean annual precipitation or as the length of the dry season (number of months < 100 mm of rain). Unfortunately, this comparison is somewhat flawed—the individual datasets represent distinct areas and sampling efforts. It still seems hardly imaginable, however, that this very clear picture is just an artifact because it is so consistent with our entire knowledge on epiphyte biology (see, e.g., Chap. 5 or Gentry and Dodson 1987).

Some types of tropical vegetation are little studied in regard to their epiphyte flora. For example, apart from a number of studies in Brazilian Cerrado (e.g., Bataghin et al. 2012), there are few studies about epiphytes in other (wet) savannas (e.g., Gottsberger and Morawetz 1993) and associated vegetation elements such as gallery forests (e.g., Schaijes and Malaisse 2001; Silva et al. 2010). Such descriptive studies can yield interesting observations. For example, in a mosaic of tropical dry forest and savanna patches in Mexico, epiphytes were entirely absent from the latter (Pérez-García and Meave 2006). Whether this exclusion is due to microenvironmental differences, due to a lack of suitable host species or, possibly, fire in the savanna is an open question. Also little studied are the epiphytes of white sand vegetation. In a rare report about such a system by Coomes and Grubb (1996), the focal epiphyte assemblages near La Esmeralda (Venezuela) were species-poor and abundances were low (c. 400 epiphytes ha^{-1}). Last but not least, mangroves are a forest type of considerable spatial extension, but the available reports paint a contrasting picture of the suitability of mangrove trees as hosts. While some mangrove forests are largely shun by epiphytes (Gómez and Winkler 1991), which could be related to, e.g., host tree characteristics or to exposure to salt spray (Zotz and Reuter 2009), other mangrove forests seem to host quite species-rich assemblages of vascular epiphytes (Giesen et al. 2007). The epiphytes of all these systems certainly deserve more attention for a full description, let alone a mechanistic understanding of local, regional, and global diversity patterns.

Among the main rainforest regions, Africa stands out with its relatively low plant richness (Primack and Corlett 2005) and a similarly low number of epiphytes. The analysis presented in Fig. 3.1, which is restricted to orchids and ferns/fern allies, agrees with the earlier quantitative assessment by Madison (1977): the African continent has less than 20 % of the epiphyte diversity of the New World and just about 25 % of the number of species found in tropical Australasia. Gentry and Dodson (1987) discussed possible reasons in some detail. They discarded several suggestions made by Madison (1977) to explain the remarkable epiphyte diversity in the Neotropics. For example, they agreed that extensive cloud forest habitats in the Neotropics promote epiphytism, but argued correctly that this cannot explain the continental differences in species richness in lowland habitats. Second, the historical *accident* of a Neotropical origin of important epiphyte families like Bromeliaceae, Cactaceae, or Cyclanthaceae as such does not offer much explanatory power, because the number of families that have epiphytic members does not differ between the Paleotropics and the Neotropics (Gentry and Dodson 1987). Hence, the important difference lies in the apparently much more rapid speciation among epiphytes in the Neotropics. Gentry and Dodson (1987) offered several possible reasons for stronger radiations in this continent: (1) A larger area of wet, aseasonal forest, in which epiphytes can achieve a finer niche partitioning, should result in generally higher α diversity, (2) greater topographic heterogeneity related to the extensive Andes leads to a greater β diversity, (3) an "evolutionary explosion", where speciation particularly in orchids took place at a fine "sympatric" scale, associated with extreme ecological dynamics, which is again bound to the existence of the Andes. Finally, they (4) contemplated a link between generally lower soil fertility in tropical Asia and epiphyte diversity and biomass. Most of these assertions remain untested almost three decades after their original publication. The "evolutionary explosion" hypothesis, however, has recently been evaluated in a meta-analysis in which Phillips et al. (2012) compared the mean levels of population genetic differentiation among orchids with other, diverse families (e.g., Asteraceae, Fabaceae, or Poaceae) and between rare and common orchid species. The results provide little support for Gentry and Dodson's (1987) notion that genetic drift in isolated populations has played a major role in their diversification.

Large-scale comparisons can easily conceal substantial regional heterogeneity. A detailed analysis of Neotropical epiphyte diversity by Cascante-Marin and Nivia-Ruiz (2013) revealed modest variation at the family level between the epiphyte floras of eight countries from South America, Central America, and the Caribbean, whereas the epiphyte quotients varied more than fivefold and the generic composition was also quite distinct. Ecuador was identified as the most diverse Neotropical locality with a stunning 4300 epiphytic angiosperm species, representing 28 % of the total flora and 38 % of all endemics. Within the New World, these authors recognized four geographic groups of epiphyte floras, i.e., the northwestern Andean region, the southern Mesoamerican region, the northern Mesoamerican region, and the island of Cuba. However, this scheme suffers from the choice of political entities as reference areas and is strongly biased by the selection of the analyzed floras. Since neither the Amazon region, nor the Atlantic rainforest, nor the South-temperate regions of the Americas were included, future studies may arguably come to different conclusions. The overall geographic heterogeneity in epiphyte diversity, however, is likely to be confirmed.

Islands lend themselves to analyze distributional differences compared to soil-rooted flora. Dust-like seeds, which are so distinctive for major epiphyte groups (particularly orchids and ferns), arguably promote far-distance dispersal, which could lead to a relatively species-rich epiphyte component of island floras. To date, the available evidence does only partly support this notion. We do know, e.g., that orchids were among the first to colonize the newly emerged Krakatau islands (Partomihardjo 2003), about the similarity of orchid floras of distant Caribbean islands (Trejo-Torres and Ackerman 2001), and about the high proportion of fern species in the floras of remote oceanic islands (Tryon 1970), which all demonstrate a high capacity for long-distance dispersal. Dassler and Farrar (2001) finding that there is no increase in the epiphyte ratio of the fern floras of islands compared to mainland regions indicates the dispersal abilities of epiphytic and terrestrial ferns do not differ. However, there was a significantly higher proportion of species with gemmiferous gametophytes (Chap. 4). The island of Cuba shows a particularly *low* epiphyte quotient compared to several mainland locations (Cascante-Marin and Nivia-Ruiz 2013). One possible reason discussed by these authors is the frequent occurrence of hurricanes (Sect. 7.3.2), because repeated dislodging of epiphytes can promote local extinctions (Migenis and Ackerman 1993). It would be instructive to compare hurricane-struck regions on the mainland and the islands of the Caribbean to test this as yet unverified suggestion (see Sect. 7.3.2).

To conclude, relative little progress has been made on the systematic quantification and mechanistic understanding of the global distributional pattern of vascular epiphytes since the seminal paper by Gentry and Dodson (1987). However, considering the massive improvements in the setup of relevant databases and the rapid developments in other organismal groups (e.g., Jetz et al. 2012) the time is ripe for a major advancement in the description and analysis of macroecological patterns of vascular epiphytes in the near future.

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Functional Anatomy and Morphology

4

The study of vegetative morphological and anatomical traits can yield valuable insights into the ecology and evolutionary history of an organism, especially when directly linked to function. A number of traits have been suggested as rather distinctive for, or at least particularly common among, vascular epiphytes when compared to soil-rooted flora (Benzing 1986, 2012). Among these are impounding structures (e.g., phytotelmata in bromeliads), litter-collecting structures (e.g., leaf rosettes in *Asplenium* species or trap roots in many Catasetinae), and special absorptive structures (the velamen radicum in orchids and some other groups, or absorptive leaf scales in bromeliads). This chapter describes many of these features in detail. In the absence of phylogenetic analyses, it usually remains unclear whether a feature really represents an adaptation, or whether previously evolved traits simply proved to be advantageous in an epiphytic environment, as (probably) in the case of impounding tanks or absorbing scales in bromeliads. For that reason, I usually avoid the terms "adaptation" or "adaptive" altogether. Hedenäs' (2012) work is an example of the type of studies that are necessary to allow unambiguous interpretations of evolutionary trends: these authors provide a rigorous statistical evaluation of differences in the frequencies of character states associated with the occurrence of bryophytes in epiphytic and terrestrial habitats. Another example is Huttunen et al.'s (2012) study on the moss order Hypnales. For three traits, evolutionary rates of dual character-state changes indicate that habitat shifts occurred prior to changes in morphology, i.e., that traits found in epiphytic taxa evolved as adaptations to the new habitat.

4.1 Plant Size

Epiphytes are generally depicted as "small bodied" (Benzing 2012), and some have even called small body size an "adaptation" to epiphytism (Nieder and Barthlott 2001). "Vegetative reduction" is unquestionable in leafless orchids (Fig. 4.1,

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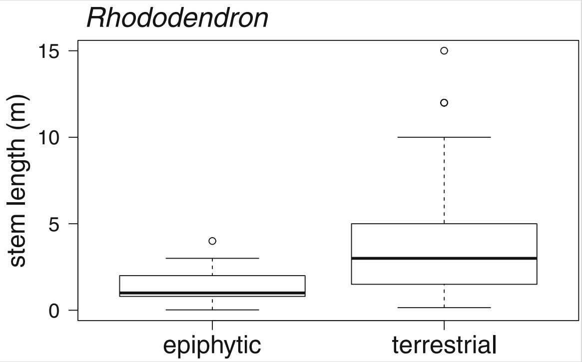
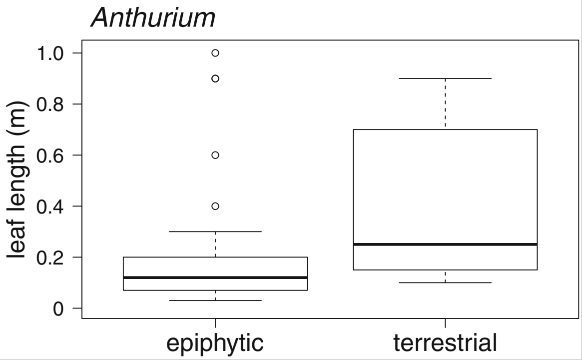
Fig. 4.1 Hundreds of epiphytic orchid species are leafless (e.g., all species of the genera *Dendrophylax*, *Microcoelia*, *Taeniophyllum*, Carlsward et al. 2006), and roots do not only carry out water and nutrient uptake, but also replace leaves as principal photosynthetic organs. Many of them are miniatures such as the shown fruiting *Taeniophyllum coxii*. The infructescence measures about 1 cm (Photograph: Wilhelm Barthlott)

Carlsward et al. 2006), rootless *Tillandsia* species (Benzing and Ott 1981), or dwarfish filmy ferns (Dubuisson et al. 2013), but rigorous quantitative studies on body size reduction as a general principle among vascular epiphytes are rare. The crucial question whether epiphytic members *within* a given clade are really smaller than soil-rooted relatives is largely unexplored. One of the few studies with a quantitative assessment of plant size distributions within a clade is the work by Creese et al. (2011) on the fern flora of Hawaii. Epiphytically as well as lithophytically growing ferns were found to be significantly smaller than terrestrial ones. Another comparison of terrestrial and epiphytic species yielded a opposing result, but this case is based on only six terrestrial and one epiphytic species: the average biomass of epiphytic *Utricularia quelchii* was almost two orders of magnitude higher than that of all the terrestrial conspecifics (Porembski et al. 2006). Given the paucity of published analyses and the relative ease of such comparisons, I haphazardly picked three genera of important angiosperm families with epiphytes and compared the size ranges of epiphytic and terrestrial species (Box 4.1). Overall, these data support the notion that among closely related species, epiphytic taxa tend to be significantly smaller.

Box 4.1 Life form and Plant Size (Gerhard Zotz, Niklas Buhk, and Christoph Hahn)
Using values from the literature, the relationship of plant size and life form was explored for three important epiphytic genera. We chose two herbaceous genera (*Sobralia*, Orchidaceae, all species from Panama and Costa Rica, and all Panamanian species of *Anthurium*, Araceae) and a woody genus (*Rhododendron*, Ericaceae, all species of the subgenus *Vireya*), representing three of the most important angiosperm families with epiphytes. All facultative species were excluded.

In the case of *Rhododendron* and *Anthurium*, epiphytic congenerics are indeed smaller (*Rhododendron*: Wilcoxon U test, $p < 0.001$, median 1.0 m, $n = 37$ species versus 3.0 m, $n = 96$ species, data from Argent 2006; *Anthurium*: Wilcoxon U test, $p < 0.01$, median stem length 0.12 m, $n = 51$ species vs. 0.25 m, $n = 12$ species, data from Croat 1986; an extreme outlier among the epiphytes (*A. clavigerum* with up to 2 m long leaves) was omitted from the graph for clarity). In the third comparison within the orchid genus *Sobralia* epiphytic taxa are statistically indistinguishable from ground-rooted species (Wilcoxon U test, $p = 0.9$, median stem length 0.47 m, $n = 12$ species versus 0.36 m, $n = 9$ species, data from Hammel et al. 2003).





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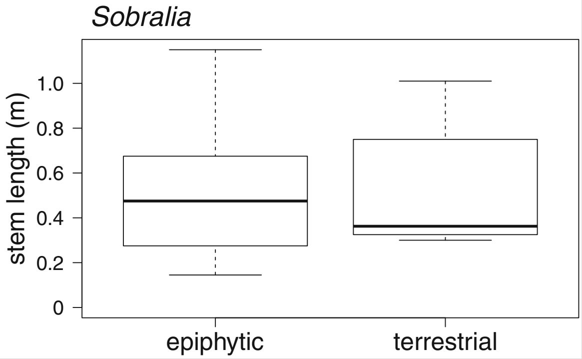
Box 4.1 (continued)



Conclusion: together with published evidence (Porembski et al. 2006; Creese et al. 2011), these three intrageneric comparisons support the notion that epiphytes are generally, but not universally, smaller than closely related terrestrial species.

4.2 Shoot Architecture

Epiphytic growth in tree crowns offers some challenges, but also advantages, for particular body plans. No quantitative analysis is available to decide whether, e.g., a sympodial organization of the shoot is really more common among epiphytes than among terrestrial taxa within a given clade (Benzing 2012), but a scandent or even pendant habit of vegetative shoot and/or inflorescence (Figs. 2.1 and 4.2) are certainly much more common in arboreal situations (and among lithophytes). The same is true for a rich development of adventitious roots (Fig. 4.11), which allow anchorage when exploring the three-dimensional matrix of the host's trunk and branches.

Many epiphytic orchids, but relatively few terrestrial species, have pseudobulbs, i.e., characteristically thickened stems (Fig. 4.3). Figure 4.4, which is based on the phylogeny of Freudenstein and Chase (2015), illustrates the occurrence of pseudobulbs within the species-rich subfamily Epidendroideae. Pseudobulbs, which are found in roughly half of all genera, are largely absent in the basal clades of the subfamily. The massive appearance of pseudobulbs coincides with the shift from terrestrial to epiphytic habit. However, the pseudobulb was subsequently lost and regained in several clades without a similar change in habitat. Some functional aspects associated with the possession of this thickened stem are discussed in Chap. 5, although the role of pseudobulbs in whole plant fluxes of water, nutrients, and carbon has received relatively little attention (Ng and Hew 2000; Hew and Ng 1996; Zimmerman 1990).

Fig. 4.2 Pendant habit of shoots and inflorescences. Attachment on tree trunks and branches allows both shoots and inflorescences to be pendant. (**a**) The dangling infructescences of two *Notylia* (Orchidaceae) plants, (**b**) pendant individuals of *Rhipsalis teres* (Cactaceae) (Photograph b: Wilhelm Barthlott)

Vessels are ubiquitous in epiphytic and terrestrial orchids, but occur much more commonly in the shoots of epiphytic taxa (Cheadle and Kosakai 1982). Since there has been no follow-up study on this observation, it is currently unclear whether this finding, which is based on the examination of 127 species, can really be generalized for Orchidaceae. In any case, the functional implications remain elusive.

Modifications of the shoot (actually of the lowermost portion, the hypocotyl) are not only found in epiphytic orchids, but also in other families such as Ericaceae (e.g., in *Macleania rupestris*, Fig. 2.2d) or Rubiaceae (*Myrmecodia* sp., Fig. 8.8). The primary function of the lignotubers in Ericaceae is assumed to be water storage (Fig. 2.2d, Evans and Vander Kloet 2010), while the tubers in rubiaceous epiphytes, which possess a system of cavities (Fig. 8.8), are the structural basis of a well-known case of ant–plant symbiosis (Chap. 8, Huxley 1980).

The bromeliad tank is certainly the most effective form of an impounding structure among epiphytes (Fig. 4.5). Similar to absorptive scales, impounding leaf rosettes are also found in terrestrial members of the genus *Brocchinia*, which is sister to all other bromeliads. Recent phylogenetic analyses suggest that the tank evolved several times independently in this family (Givnish et al. 2014). Although not restricted to epiphytes, impounding tank and epiphytic lifestyle are undoubtedly closely correlated in Bromeliaceae, and this morphological feature has probably contributed substantially to the impressive radiation as a key innovation, particularly in the subfamily Bromelioideae. Benzing's (2000) monograph on the Bromeliaceae gives detailed information on different tank forms within this family. He distinguishes five ecological types primarily based on the presence and

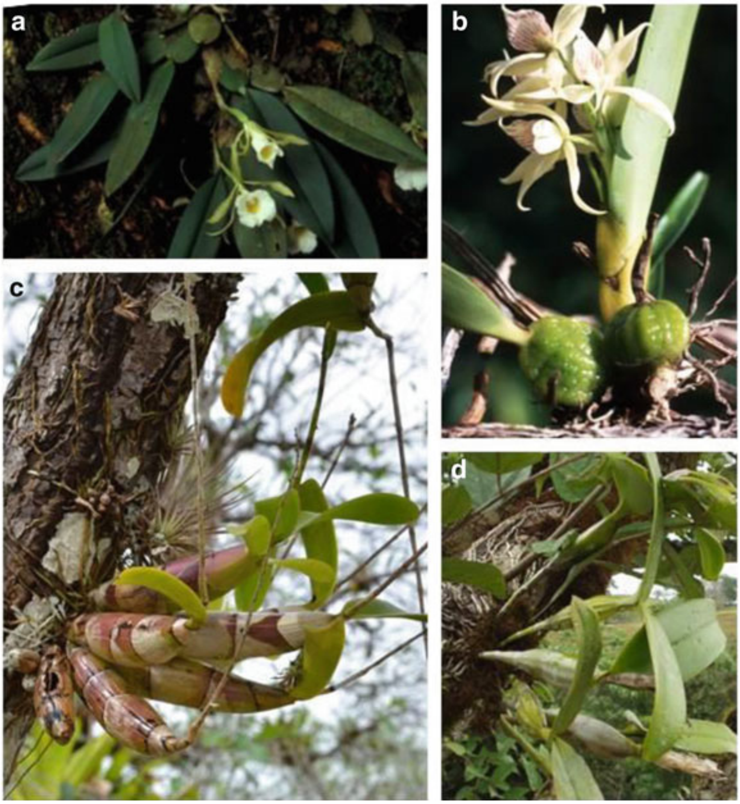


Fig. 4.3 Pseudobulbs are common among epiphytic orchids. Four typical shapes are shown: (**a**) oblong-elliptic, flattened (e.g., *Trichopilia*), (**b**) ovoid (e.g., *Prosthechea*), (**c**) cylindrical and hollow (e.g., *Caularthron*), and (**d**) fusiform (e.g., *Cattleya*)

distribution of absorptive scales and on the degree of dependence on roots for water and nutrient acquisition (Table 4.1). In epiphytic tank bromeliads of types III and IV, in which roots are believed to serve almost exclusively as holdfasts (but see, e.g., Petit et al. 2014), there is usually a gradual differentiation along the longitudinal leaf axis in respect to form (e.g., in stomatal and trichome density, Reyes-García et al. 2008) and function (e.g., CAM activity, Freschi et al. 2010). At a qualitative level, there is a good understanding of the "typical" habit of tillandsioids of types IV and V from mesic, semi-mesic, and xeric growing sites (Table 4.1, Gilmartin and Brown 1986), but a more rigorous quantitative evaluation is lacking; i.e., our understanding of the functional consequences of the many different architectures in Bromeliaceae on the effectiveness of water catchment and storage as well as on light capture and carbon gain is still very sketchy (e.g., Zotz and Laube 2005; Zotz et al. 2002).

Impounding structures among epiphytes are not restricted to bromeliads, but their presence in taxa like *Collospermum* (Asteliaceae) or *Cochliostema*

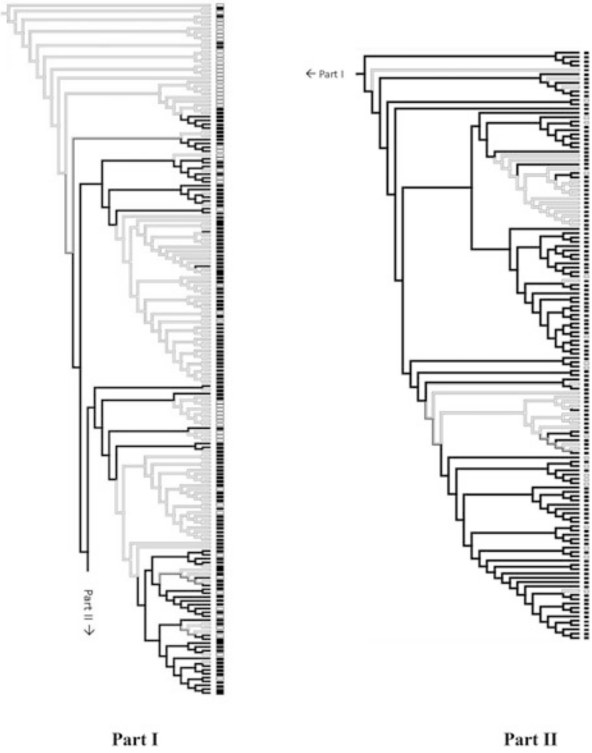


Fig. 4.4 Occurrence of pseudobulbs in the subfamily Epidendroideae (Orchidaceae). The most parsimonious reconstruction of the evolution of pseudobulbs is based on the phylogeny published by Freudenstein and Chase (2015). Information on the occurrence of pseudobulbs in the genera was obtained from (Pridgeon et al. 2005, 2009, 2014). The character-state "pseudobulb" is indicated by *thick black lines*. The incidence of epiphytism (*black boxes*) was taken from Zotz (2013)

(Commelinaceae) has received very little attention in this regard (Wardle et al. 2003). Some aspects of the anatomy and morphology of *Cochliostema odoratissimum*, which resembles the typical bromeliad tank to an even higher degree than *Collospermum*, have been studied by Troll (1961). These plants have no absorbing scales; hence the plants probably benefit from their tank in the same way as some less specialized tank bromeliads, i.e., via conventional root uptake (Type II/III sensu Benzing 2000, compare Table 4.1). Other well-known examples for impounders are epiphytes with bird-nest architecture such as *Asplenium nidus* (Aspleniaceae) or some *Anthurium* and *Philodendron* (Araceae) species (Zona and Christenhusz 2015). Heterophyllous ferns (e.g., *Drynaria* sp., Polypodiaceae) achieve the same function with special nest fronds, which form a detritus-collecting basket. *Nepenthes* (Nepenthaceae) pitchers should also be mentioned in this context although there is no reason to assume any differences in form and function compared to the more common terrestrial congenerics (Barthlott et al. 1987). Unfortunately, little quantitative information is available on the functional consequences of all the structures mentioned in this paragraph, neither for the plants themselves nor for neighboring plants because of, e.g., nutrient enrichment of the stemflow (e.g., Turner et al. 2007; Kale and Dongare 2007).

Atmospheric nutrition, sometimes accompanied by vegetative reduction (sensu Benzing and Ott 1981) to the point of almost complete loss of roots or stems, leads

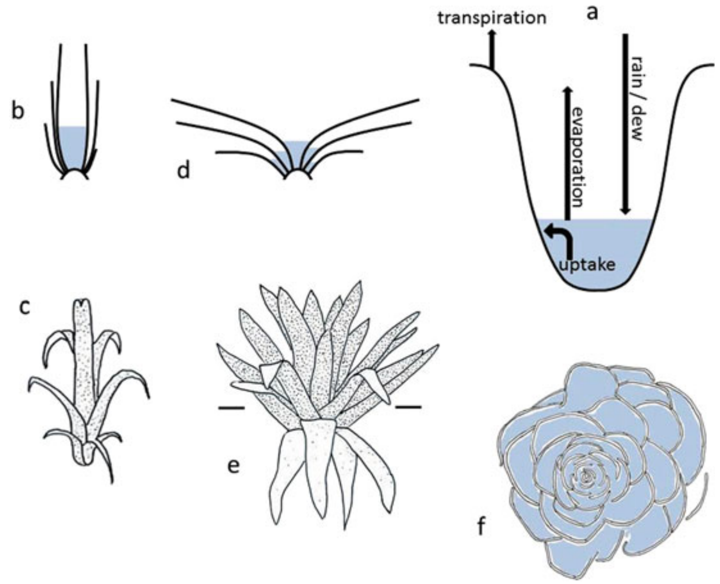


Fig. 4.5 Bromeliad tanks come in many different shapes, but a detailed analysis of the functional implication in terms of the effectiveness of water capture, possible trade-offs with carbon gain (e.g., due to self-shading) is missing. (**a**) Shows a simplified model, outlining the processes in these microlimnetic systems: input by rain and dew, output by evaporation and plant uptake, which compensates transpirational water loss). Two tank types (single-chambered and multiple chambered) are presented as habit sketches (**b**, **d**) and drawings of real plants (**c**: *Billbergia* sp.; **e**: *Vriesea* sp.). (**f**) A cross section of a shoot of *Guzmania monostachia* (approximately at the height indicated by the *lines* in **e**) with numerous water-filled leaf bases. *Shaded areas* indicate water

Table 4.1 Five ecological types of the Bromeliaceae sensu Benzing (2000)

Type	Root system	Shoot	Foliar trichomes	C3/ CAM	Habit
Type I	Absorptive	No phytotelmata	Nonabsorptive	C3/ CAM	Terrestrial
Type II	Absorptive	Weakly developed phytotelmata	Absorptive on leaf bases	CAM	Terrestrial
Type III	Mechanical to conditionally absorptive	Well-developed phytotelmata	Absorptive on leaf bases	Mostly CAM	Variable
Type IV	Mechanical to conditionally absorptive	Well-developed phytotelmata	Absorptive on leaf bases	Mostly C3	Mostly epiphytic
Type V	Mechanical or missing	No phytotelmata	Absorptive over entire shoot	CAM	Mostly epiphytic

to a very different body plan, e.g., the so-called atmospherics, in Bromeliaceae. Benzing (2000) provides a lucid account on the different body plans in this family.

4.3 Gametophytes of Epiphytic Ferns

It is frequently overlooked that the alternation of generations in ferns includes two free-living generations, a haploid gametophyte and a diploid sporophyte. Most studies focus on the larger sporophyte; the usually tiny gametophyte has received relatively little attention. As pointed out by Farrar et al. (2008), many textbooks paint a simplistic and misleading picture by disregarding the large variability in gametophyte morphology. Considering that the gametophyte not only controls genetic diversity as the gametangia-producing phase, but also controls recruitment and habitat selection, this neglect is surprising. Farrar et al. (2008) provide a detailed account on all aspects of the biology of fern gametophytes and indeed identify a number of differences between epiphytic and terrestrial ferns. In contrast to the typical terrestrial gametophyte, which is heart-shaped and short-lived, gametophytes of epiphytic taxa usually have a strap-like or ribbon-like morphology, sometimes produce gemmae as a means of vegetative reproduction, and are invariably long-lived. Clearly, a better understanding of gametophyte-level strategies in morphology and physiology is needed to appreciate the mechanistic basis of the successful conquest of the epiphytic habitat by ferns (Watkins et al. 2007).

4.4 Leaves

There is no shortage of theories *and* empirical evidence on the relationship of leaf traits such as leaf area, specific leaf area (SLA), leaf dry matter content, succulence, or stomatal density, and environmental conditions (e.g., Parkhurst and Loucks 1972; Grime 2001; Wright et al. 2004; Boardman 1977). For example, Wright et al. (2004) introduced the “worldwide leaf economics spectrum”, a universal relationship for all plants, which reflects a fundamental trade-off between traits associated with high rates of resource acquisition in productive habitats and those traits associated with resource retention under unfavorable conditions. Although this and other conceptual frameworks immediately allow the development of testable quantitative predictions for these traits in vascular epiphytes, this research opportunity is virtually unexplored. This contrasts with research on other ecological groups. For example, Pierce et al. (2012) studied leaf trait variation in hydrophytes in comparison to “typical” terrestrial plants, as did Farnsworth and Ellison (2008) with carnivorous plants, both with highly interesting results. For epiphytes, however, we are mostly left with rather qualitative statements on leaf traits, e.g., “epiphyte foliage tends to be tougher, more damage-resistant and longer-lived” (Benzing 1990). Given the overwhelming importance of water for the epiphytic existence, there are many immediate expectations for key leaf traits such as leaf size, degree of succulence, or stomatal and trichome frequencies, each discussed in more detail below.

Leaf Size Theory makes clear predictions about leaf size in drought-prone environments (Parkhurst and Loucks 1972) and we should expect epiphyte leaves to be relatively small. Indeed, published studies on two different groups of ferns (Dubuisson et al. 2003; Creese et al. 2011) support this notion: leaves of epiphytic taxa within these clades tend to be smaller (Fig. 4.6). However, there is also contrasting evidence: I reviewed the available information on leaf size for all obligate epiphytes and terrestrial congenerics of *Rhododendron*, subgenus *Vireya* (Ericaceae). Leaf areas varied over more than 3 orders of magnitude from 1 cm^2 to c. 1200 cm^2, but the median leaf area was statistically indistinguishable between life forms (Wilcoxon U test, $p = 0.39$, $n = 37$ epiphytic species and 96 terrestrial species, data from Argent 2006). Although plausible, the expectation of a generally smaller leaf size in epiphytes is only partially supported by the current data base.

Leaf Form Variation in leaf form is well studied in Orchidaceae. The non-articulate plicate leaf type of most terrestrial orchids probably represents the ancestral condition in this family, whereas there is a trend toward articulate and conduplicate leaves among epiphytic taxa (Dressler 1981). Cameron (2005) conducted a study on the relationship of leaf type and life form in the tribe Malaxideae, which is an orchid tribe with a large number of both obligate epiphytes and obligate terrestrial species, and thus ideally suited for such a comparison. Epiphytic species had either unifacial leaves arranged as a fan or bifacial, linear, conduplicate leaves. Terrestrials, in turn, had either plicate or 1–2, usually rounded, conduplicate leaves. Notably, both epiphytic growth and conduplicate leaves are plesiomorphic in this tribe; hence the plicate leaves in extant terrestrials represent two switches of this character state. In bromeliads, broad, imbricate leaves and

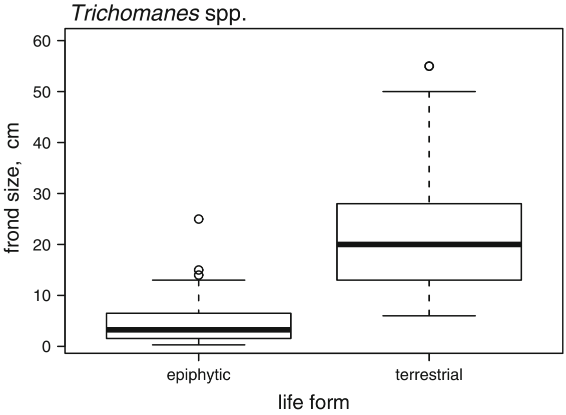


Fig. 4.6 Comparison of frond lengths (in cm) in 166 epiphytic and terrestrial *Trichomanes* species. The differences are highly significant (median: 3.2 cm (epiphytes) vs. 20 cm (terrestrials), U-test, $p < 0.001$). Data from Dubuisson et al. (2003)

narrow, linear leaves are closely associated with two extreme ecological types, the tank form and the atmospheric form (Benzing 2000).

Leaf Tissue Types Leaf succulence due to large, water-rich parenchyma cells is common in epiphytic members of many families, e.g., Orchidaceae (Dressler 1981), Bromeliaceae (Horres and Zizka 1995), or Melastomataceae (Reginato et al. 2009). Also noteworthy is an adaxial multiple epidermis in *Peperomia* (Piperaceae). Although not restricted to epiphytic members but typical for the entire genus of *Peperomia*, Kaul (1977) held this xeromorphic feature to be most prominent among epiphytic members. Intraspecific variation in hydrenchyma thickness is not uncommon (Chiang et al. 2013; Godoy and Gianoli 2013). For example, in the epiphytic fern, *Pyrrosia lanceolata* (Polypodiaceae), the hydrenchyma in seven sites along a precipitation gradient in Taiwan increased significantly with the mean number of rainless days in the dry season (Chiang et al. 2013).

Foliar sclerenchymatous elements, e.g., tracheoids, which supposedly prevent the collapse of soft tissue in times of water stress, are common in many epiphytic taxa (Oliveira and Sajo 1999; Pereira et al. 2011; Yukawa and Stern 2002; Rao and Bhattacharya 1977). Differences in sclerenchyma types in epiphytic and lithophytic *Cymbidium* (Orchidaceae) species were identified by Yukawa and Stern (2002) as were differences in vein density in 30 epiphytic and terrestrial fern species (Zhang et al. 2014).

Stomata Stomata are fundamental for plant water relations because of their role in the regulation of transpiration. Their density, size, and responsiveness to environmental factors strongly affect water loss of a leaf. Similar to ground-rooted flora, the leaves of the majority of epiphytic orchids and bromeliads are hypostomatic, although a considerable number of species with amphistomatic leaves exist (compare, e.g., Meisner et al. 2013; Williams 1979). Rasmussen (1987) noted that many structural features of orchid stomata are decidedly xeromorphic, e.g., well-developed outer cuticular ledges, thickened guard cells, and narrow substomatal chambers. However, the available information does not always support the notion of consistent anatomical differences between arguably more drought-stressed epiphytic flora and ground-rooted plants. For example, while Paek and Jun (1995) confirmed earlier findings that the stomata of epiphytic orchids are generally smaller than those of terrestrial family members (summarized in Rasmussen 1987), there are also studies with conflicting evidence (Yukawa and Stern 2002).

Stomatal densities are typically low. Johansson (1974) reports an average of 60 stomata mm^{-2} for 19 epiphytic orchids, while stomatal densities in epiphytic bromeliads (e.g., Adams and Martin 1986; Meisner et al. 2013; Reyes-García et al. 2008) are even lower, ranging from 6 to 43 stomata mm^{-2}. Extremely low densities were found in *Tillandsia bryoides* (0.1 stomata mm^{-2}, Evans and Brown 1989). Overall, such stomatal densities are comparable to succulents in xeric habitats and much lower than those found in typical terrestrial herbs (Larcher 2003). A functional link between low stomatal density and epiphytic growth is also indicated by comparisons of epiphytic and ground-rooted conspecifics of hemiepiphytes, e.g., of the genus *Ficus* (Moraceae). The latter have typically 2–4 times higher stomatal densities (Holbrook and Putz 1996; Schmidt and Tracey 2006). Conversely, some multispecies comparisons found no difference among epiphytic and terrestrial orchids (Paek and Jun 1995), while stomatal densities of obligate and facultatively epiphytic *Paphiopedilum* species were even higher than those of terrestrial congenerics (Zhang et al. 2012).

Trichomes The foliar trichomes of Bromeliaceae are multicellular structures in the leaf epidermis consisting of a living stalk and a dead shield (Fig. 4.7, Benzing 2000). Their role in the uptake of water and nutrients was already noted by the earliest students of epiphytes (e.g., Schimper 1888). Benzing (2000) gives an excellent account of their morphological diversity and absorptive function, not disregarding other roles (e.g., photoprotection, Pierce 2007). A gradient in trichome density along the longitudinal leaf axis mentioned above (Sect. 4.2) is not found universally (reviewed by Meisner et al. 2013), but scale shape and density differ substantially among species (Fig. 4.7). In addition, different environmental conditions cause intraspecific variation. For example, Dimmit (1985) documents a substantial increase in trichome cover in *Tillandsia caput-medusae* when growing in bright, arid habitats.

Plants in many other families possess leaf scales as well, but trials to assign particular functions to them are rare. Earlier assertions that, e.g., the glandular trichomes of pleurothallid orchids are absorptive and functionally equivalent to bromeliad scales (Pridgeon 1981) were later shown to be premature (Benzing and Pridgeon 1983). Recent propositions (Benzing 2012) of an absorptive function of leaf scales in other plant groups, e.g., in the fern *Pleopeltis polypoidoides* or in impounding *Astelia* sp., remain untested. Thus, current knowledge suggests that bromeliad scales are unique in their absorptive function. However, it is still unclear whether they represent an “adaptation” to the epiphytic habitat, because they are also found in terrestrial *Brocchinia* species, which grow in wet, extremely infertile habitats of the tepuis and adjacent sand plains of the Guayana Shield (Givnish et al. 2007). Most recent evidence reported by Givnish et al. (2014) does not entirely resolve the issue but lends additional support to the notion of parallel evolution. Absorptive trichomes would thus show the same pattern of correlated evolution with epiphytism as tanks. A similar evolutionary link of epiphytic existence and stalked scales was proposed by Tsutsumi and Kato (2008) for obligate epiphytes in the genus *Davallia* and other Polypodiaceae. However, in this case the function is unclear.

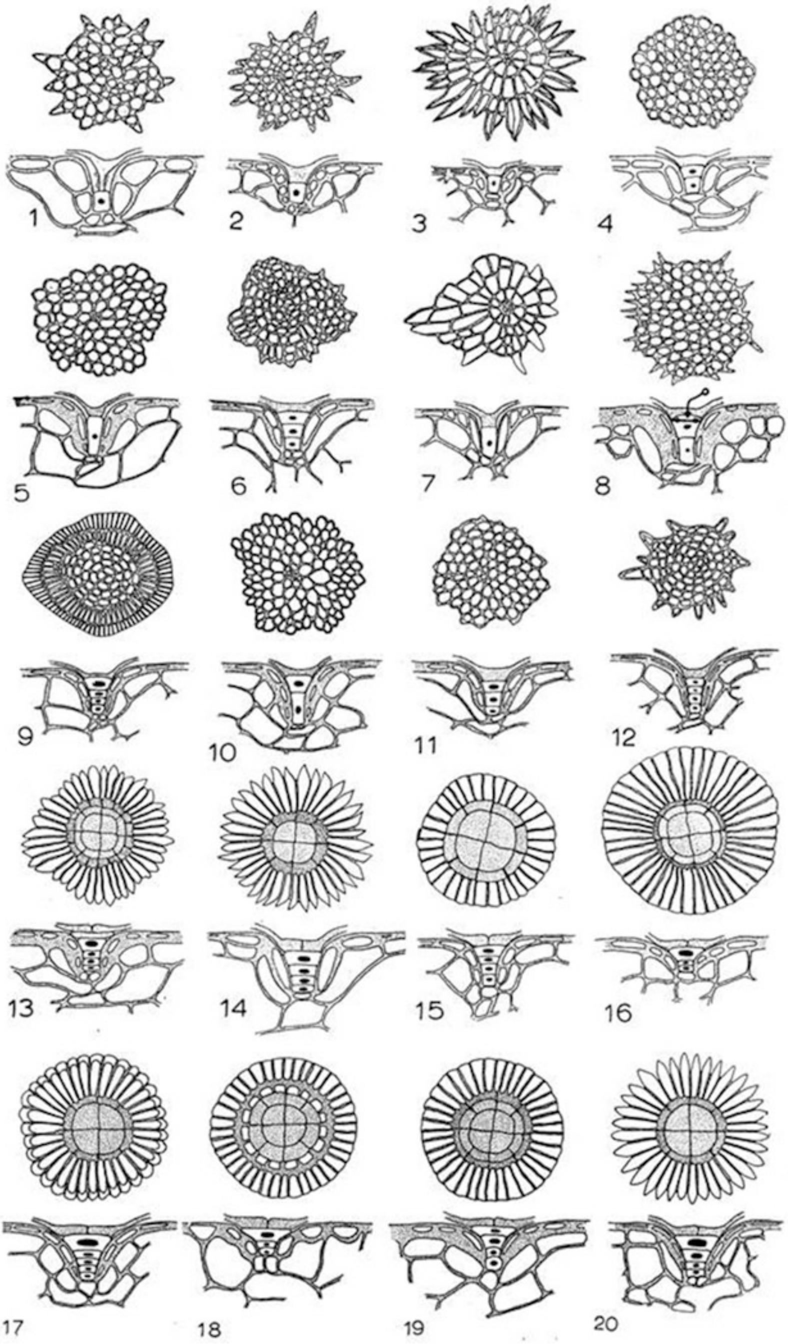


Fig. 4.7 Morphological variation in foliar trichomes of bromeliads. Shown are caps and stalks of 20 species (Benzing and Burt 1970). Note that the magnification differs almost tenfold. For more details, see Benzing and Burt (1970). Reproduced with permission

4.5 A Special Case: Heteroblasty

Heteroblasty, which describes an abrupt change in gross morphology, e.g., in leaf size, leaf shape, or phyllotaxis, during ontogeny (Fig. 4.8, Zotz et al. 2011), is quite common among bromeliads, although information on the exact frequencies is not available. The traditional interpretation asserted that seedlings of heteroblastic species develop into so-called atmospherics with narrow, lanceolate leaves, densely covered with trichomes, which years later change rather abruptly into plants with an impounding tank formed by overlapping, broad leaf bases (Benzing 2000). The two succeeding ontogenetic forms appear analogous to xerophytic species such as *Tillandsia recurvata* and mesic species with a tank such as *Tillandsia utriculata*. Considering that the effectiveness of a tank is very low in small plants (Sect. 5.2, Fig. 5.4, Zotz and Thomas 1999), this suggests that (1) atmospheric juveniles are important in the context of drought resistance and (2) atmospheric species may be derived evolutionarily from mesic predecessors via neoteny (Tomlinson 1970). The actual evidence for this scenario (Benzing 2000) was primarily taken from studies with two species, heteroblastic *Tillandsia deppeana* and *Vriesea geniculata* (Adams and Martin 1986; Reinert and Meirelles 1993). Unfortunately, these studies did not take into account possible, more continuous changes in morphology and anatomy related to ontogenetic drift (Evans 1972), but compared *small* plants (atmospherics) with *large* plants (tanks). Indeed, a detailed study with 17 species of 5 genera including the entire size range from smallest atmospheric to largest tank individual revealed that most of the variation in trichome density, stomatal density, or hydrenchyma thickness was actually not related to the switch from atmospheric to tank, but represented a continuous change during ontogeny (Meisner et al. 2013). As an additional complication, the direction of these ontogenetic changes was not always the same. This increases the challenge to produce a convincing functional interpretation of heteroblasty in Bromeliaceae.

Another, even less investigated, case of heteroblasty among epiphytes is found in many twig orchids (Chase 1986). In the majority of the species related to *Rodriguezia* or *Leochilus*, adult individuals have pseudobulbs and conduplicate

Fig. 4.8 Heteroblastic changes in *Vriesea heliconioides*. (**a**) Juvenile with narrow leaves, (**b**) plants in transition with both narrow and broader leaves and (**c**) later, adult stages with broad leaves forming a tank. The scales consistently indicate 5 cm

Fig. 4.9 Many twig orchids have a psygmoid habitat, at least as juveniles. Shown are *Erycina pusillum* (*left*) and *Erycina glossomystax* (*right*). Leaves of *Erycina pusillum* are typically 2–6 cm long (Photograph: Wilhelm Barthlott)

leaves, while juveniles show a psygmoid habit (Fig. 4.9) with laterally flattened leaves. Considering the extreme growth conditions of these plants in the very periphery of tree crowns, it seems very plausible to assume that the juvenile habit is advantageous in conserving moisture and nutrients, but this hypothesis, which was originally put forward by Chase (1986), has never been rigorously tested.

4.6 Roots

Roots face rather extreme challenges in epiphytic habitats, particularly those of bark epiphytes, in which roots usually do not grow *within*, but fully exposed *on* the substrate. The best-known anatomical feature in this context is the velamen radicum. This a spongy, usually multiple epidermis of the roots with dead cells at maturity, bordering internally on an exodermis that features both thick-walled cells and so-called passage cells (Fig. 4.10, Pridgeon 1987). Although also found in an (unknown) number of terrestrial taxa (van Guttenberg 1968), it is most characteristic for the roots of epiphytic orchids, an unknown number of epiphytic *Anthurium* species and some facultative epiphytes such as *Clivia nobilis* (Amaryllidaceae). Mulay and Deshpande (1961) suggested that velamentous terrestrial taxa are derived from epiphytic groups. Reports on the occurrence of velamena in species of purely terrestrial groups, e.g., *Agave sisal* (da Cunha Neto and Martins 2012) or *Asphodelus aestivus* (Sawidis et al. 2005), do not completely falsify this notion, but certainly question its generality. In contrast to the general assertion that Bromeliaceae lack a velamen radicum, a few recent reports suggest the existence of this structure in both terrestrial and epiphytic bromeliads (e.g., Pita et al. 2002; Silva and Scatena 2011). None of these studies investigated functional aspects (compare Sect. 5.4.2). However, if their function were indeed similar to that in orchids, we may be forced to revise Benzing's ecological types, particularly types III and IV (Table 4.1).

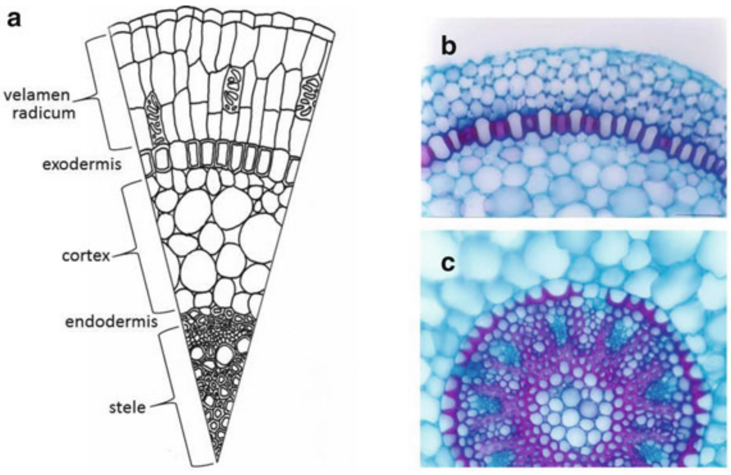


Fig. 4.10 (**a**) Semi-schematic cross sections of aerial orchid root. (**b**) Details of the exodermis of *Epidendrum secundum*, which separates cortex and velamen. Note the thin-walled and enlarged passage cells. (**c**) Detail of the stele of *Dichaea cogniauxiana*, which is separated by an endodermis from the cortex. Note the *U-shaped* cell thickenings and the passage cells (Photographs: Ana Silvia Moreira)

Anatomical and morphological variation of the velamen has been studied extensively among Orchidaceae (Porembski and Barthlott 1988; van Guttenberg 1968), much less so in *Anthurium*: the most extensive treatise of roots in Araceae is still Lierau's (1888) monograph. There is a consensus that the velamen is multifunctional (Pridgeon 1987). The negative correlation of velamen thickness with moisture availability in epiphytic orchids (Sanford et al. 1973; Parrilla Díaz and Ackerman 1990) supports the view that the effective uptake of water and nutrient is not the only important role of the velamen (Went 1940; Zotz and Winkler 2013); the reduction of water loss is critical as well. Overall, however, the connection between form and function is not well established for the velamen and still largely conjectural. For example, so-called tilosomes, i.e., lignified excrescences from the innermost cell layer of the velamen adjacent to the passage cells of the root exodermis, are common in epiphytic orchids, but rare in terrestrial ones (Pridgeon et al. 1983). It is plausible that these tilosomes operate as protective plugs of the passage cells, which reduce transpiration when the velamen is filled with air as suggested by Pridgeon et al. (1983), but real evidence is not available. There are even some indications against it, because tilosomes should be more common in drier habitats, whereas Parrilla Díaz and Ackerman (1990) found them exclusively in orchids growing in wet sites. We have little quantitative data for the supposed functions in nutrient uptake (Zotz and Winkler 2013; Haas 1975), or its role in protection against excess radiation (Chomicki et al. 2015), and none on mechanical damage, and possible trade-offs between divergent functions in uptake of water and nutrients and photosynthesis are also largely unexplored. Leafless orchids (Fig. 4.1) show some features which should alleviate the problem of a triple root function (holdfast, water and nutrient uptake, photosynthesis): these roots are normally flattened and possess continuously air-filled regions of the velamen called pneumathodes (Benzing 1996).

Other anatomical features of roots deserve mention. Very narrow tracheids in epiphytic epidendroids may reduce the risk of embolism under recurring drought (Thorsch and Stern 1997). Epiphytic and terrestrial orchids differ in the possession of tracheoidal elements (Olatunji and Nengim 1980). These idioblasts with their annular, spirally thickened or pitted walls resemble tracheids, but occur outside the vascular bundles in diverse tissue of many epiphytic orchids. Only very few terrestrial species possess tracheoids, and those that do all evolved from epiphytic groups (Burr and Barthlott 1991). Such idioblasts are also frequently, but not exclusively, found in many epiphytic ferns (Leroux et al. 2011). Although tracheoids are believed to provide mechanical support, to function as water storage cells, or to maximize apoplastic transport, assertions are not based on experimental evidence, but merely on plausibility (Pridgeon 1982).

Increasing knowledge on the function of the velamen in Orchidaceae does not solve the puzzle which particular root traits support epiphytic existence in other taxa. Few studies perform rigorous quantitative analyses to identify differences in traits between epiphytic and terrestrials of a given clade, but observations are still valid starting points for future studies. For example, Reginato et al.'s (2009) study on the anatomy of *Pleiochiton* (Melastomataceae) points to the role of roots as storage organs for water. Roots in this epiphytic genus are highly succulent. In a study with different *Astelia* species, Carlquist and Schneider (2010) found hardly any differences in the tracheary element microstructure in roots of terrestrial species and scandent/epiphytic congenerics. Again, the roots were somewhat succulent compared to other monocotyledons. Studying about 50 species of Cyclanthaceae, Wilder (1986) tested the hypothesis that the aerial roots of epiphytes, being subject to frequent drying between rainfalls, have a broader circumstellar ring of sclerenchyma than terrestrial taxa to maintain functionality. Indeed, their expectation was borne out—epiphytes tended to have a broad, terrestrial taxa a narrow or no ring at all.

Some epiphytic ferns produce massive root mantles. Although most of these roots seem to be dead, Troll (1952) argued that such a mantle may play an important role in plant water relations by storing substantial amounts of water for later uptake: a leafless root–shoot system of *Asplenium nidus* (air dry weight of 2.4 kg) was able to imbibe 5 kg of water. He likened the function of the root mantle to that of the velamen, but supplied no experimental evidence. Other epiphytic groups have an extremely reduced root system, sometimes to the extent that roots are missing entirely. For example, in some Hymenophyllaceae the absorptive function of roots is taken over by rhizomes and leaves, and attachment is achieved by adhesive hairs of the rhizome (Schneider 2000). Rootlessness is also found in other epiphytes, e.g., Psilotaceae, and, at least as adult, in some *Tillandsia* species. Whether this reduction is really relevant in terms of nutrient economy as suggested by Benzing and Ott (1981) is an open question.

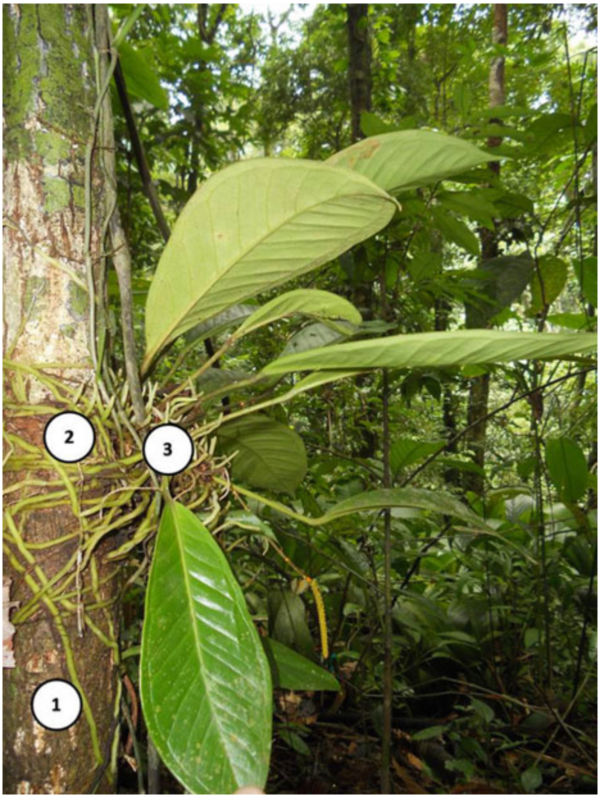


Fig. 4.11 Variation in root growth directions. Some roots of this *Anthurium acutangulum* show positively geotropic growth (1), which is typical for roots of terrestrial plants. Other roots of epiphytes follow the substrate without reference to gravity (ageotropic growth; 2) or even grow upwards, i.e., opposite to gravity (negatively geotropic growth, 3) (Photograph: Glenda Mendieta-Leiva)

In contrast to most terrestrial plant roots, which typically show positively geotropic growth (but see: Reddell et al. 1996; Sanford 1987), roots of epiphytes may show a variety of orientations (Fig. 4.11), i.e., may also respond ageotropically or even negatively geotropically, which obviously ensures effective attachment to the host tree. In some cases, the same individual plant develops different root types. For example, many epiphytic aroids produce anchor roots, which are ageotropic ("Haftwurzeln," Went 1895) and positively geotropic feeder roots ("Nährwurzeln"): for a detailed account on these different root types, see Mayo et al. (1997).

Many *Anthurium* species of the section *Pachyneurum* produce a "litter basket" of profusely branching roots characterized by negative geotropism. Such baskets can also be found in many epiphytic orchids in the tribes Cymbidieae and Maxillarieae, and Dressler (1981) suggested that this morphology allows the effective collection of fallen leaves and other debris. Anatomically, roots with negatively geotropic growth and other roots of epiphytic *Cymbidium* species only differed in the configuration of the xylem (Yukawa and Stern 2002). Although the arrangement of the conductive cells in roots with negatively geotropic growth may indicate loss of function for water and nutrient transport (Barthlott and Capesius 1975), experimental evidence for this notion is lacking.

4.7 Seed Size and Seed Morphology

Seed traits have been identified from early on as key for success or failure of the members of particular plant lineages in tree crowns. Schimper (1888) identified three groups of diaspores, (1) "dust-like" seeds (in orchids and ferns), (2) other anemochorous (=wind dispersed) seeds with various types of appendages increasing draft (e.g., in Bromeliaceae—Tillandsioideae, Rubiaceae), and (3) zoochorous diaspores (e.g., in Cyclanthaceae, Araceae, Gesneriaceae, Cactaceae). Most other seed types have hardly a chance to mitigate the action of gravity, get attached to bark, and establish successfully. However, many species, which are not growing as epiphytes, also possess diaspores that fall into one of the three categories outlined above. Thus, belonging to one of these groups is at best *necessary*, but certainly not *sufficient* for epiphytic existence. Unfortunately, we have made rather little progress toward a functional understanding beyond Schimper's description of important seed traits. There are studies which have focused on seed traits of epiphytes (e.g., Palací et al. 2004; Swamy and Kumar 2007), but mostly not in terms of a comparative and/or functional analysis. One of the few exceptions is Rockwood's (1985) comparison of the seed weights of c. 370 plant species of eight families from the Neotropics. Epiphytes in the studied groups had by no means particularly small seeds: comparing seed weight of epiphytes with those of trees, herbs, or shrubs *within* families showed consistently that seeds of epiphytes were similar or even slightly heavier than those of shrubs in, e.g., Melastomataceae or Gesneriaceae. Overall, however, epiphyte seed weights showed a bimodal distribution as expected from Schimper's categories.

A few studies directly compared seed characteristics of epiphytic and terrestrial orchids, e.g., Yoder et al. (2010) studied ten North American endemics, while Tsutsumi et al. (2007) compared seeds of six epiphytic and terrestrial *Liparis* species. The first study found seeds of epiphytic orchids to be smaller, lighter, and more porous, while the comparison of congeneric *Liparis* yielded the opposite result: epiphytes had larger seeds with smaller air volume. To date, generalizations are still difficult and it remains unresolved whether seeds of epiphytic species differ in size and other traits compared to terrestrial ones of the same clade (Arditti and Ghani 2000).

Elaters are found in the seed pods of many epiphytic orchid genera, but are almost completely absent from terrestrial genera (Fig. 4.12, Hallé 1986). The function of these elongated cells is assumed to be similar to that of the better known case of elaters in the capsules of liverworts and hornworts, where the hygroscopic movements assist in diaspore release. It remains enigmatic, however, why this feature should be restricted to epiphytic orchids.

Schimper (1888) already noted the importance of a flight apparatus for effective dispersal from tree to tree. Examples for such appendices can be found in

Fig. 4.12 An unknown number of (epiphytic) orchid species possess elaters. These elongated cells are presumed to assist in diaspore release similar to the better known case in liverworts. (**a**) Capsule of *Dimerandra emarginata*. (**b**) Detail of *yellow* seeds and *whitish* elaters of the same species (Photograph: Ralf Kulenkampff, Keyence)

Bromeliaceae, particularly in Tillandsioideae, but also, e.g., in Gesneriaceae, Rubiaceae, or Asteraceae. For one, such seed appendices improve airworthiness, but microstructures such as bifurcate cross-walls or hooks also assist in the attachment to tree bark. The extensible helical wall thickenings of the seed coat of *Chiloschista lunifera* represent a microstructure with similar function in the Orchidaceae (Fig. 4.13, Barthlott and Ziegler 1980). More recently, Wester and Zotz (2011) reported an additional function: the seed hairs of *Catopsis* seeds promoted germination by wick-like water uptake. This effect even improved the water relations of small seedlings as long as they were attached to the seed coat. Maximizing the area of contact between seed and substrate during germination is probably one of the most important factors determining the ability to germinate under tension—suggesting functional relevance of the flattened shape of many seeds (McWilliams 1974). As in many other aspects of epiphyte ecology, the general statements on dispersal ability, etc., are not yet backed up by actual data. The D^3 data bank (www.seed-dispersal.info, accessed: December 2015) with

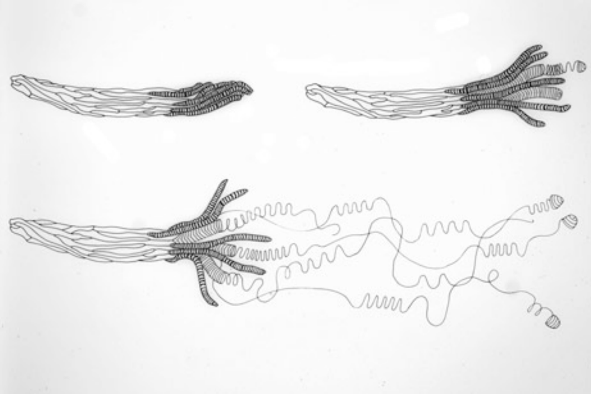


Fig. 4.13 The extensible helical wall thickenings of the seed coat of *Chiloschista lunifera* are thought to assist in the attachment of the seed to the bark. Reproduced after Barthlott and Ziegler (1980)

information on diaspore dispersal characteristics of several thousand taxa counts with just two entries of terminal velocity of seeds of Bromeliaceae (*Pitcairnia albiflos* and *P. imbricata*). A more comprehensive comparison of the dispersal characteristics of epiphytes with those of other plants is overdue.

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Physiological Ecology

5

The design of an ecophysiological study that allows strong and unambiguous inferences is always a challenge, not only when working with epiphytes. Irrespective of the expected, large *interspecific* variation, it is essential to identify all uncontrolled sources of variation to allow the correct link between the results of a particular study and complex, natural situations. For example, different genotypes may cause differences under otherwise identical conditions (Rawson et al. 1987; Geber and Dawson 1997). Such genotypic differences and/or phenotypic responses to *previous* environmental conditions may be the reason for frequently observed differences in morphology and physiology among conspecific plants growing under laboratory conditions and in situ (Inselsbacher et al. 2007; Khasim and Rao Mahona 1984; Pinheiro and de Barros 2007; Zotz and Mikona 2003). Factors rarely act in isolation, so more complex experimental designs are more telling than single-factor approaches. For example, while nutrients may be potentially limiting for many epiphytes, low water supply may be of such overriding importance under natural conditions as to make it the only *ecologically* relevant factor (Laube and Zotz 2003). Similarly, plant size has been identified as a substantial source of interspecific variation in epiphytes. A series of studies (reviewed in Zotz et al. 2001a) demonstrated considerable and consistent size-related intraspecific differences in physiological parameters in many herbaceous epiphytes (for an exception, see: Martin et al. 2004a). Thus, the choice of the studied specimens in a comparative study could seriously bias its outcome and any subsequent ecological interpretation. Examples of traits with significant size-related variation are photosynthetic capacity, leaf N, in situ leaf gas exchange patterns, long-term stomatal limitation as indicated by $\delta^{13}C$ ratios (Box 5.1), stomatal responses to drought, or hormone relations. All were regularly found to be a function of plant size, independent of a likely additional effect of, e.g., leaf or plant age. Subsequent work showed that some

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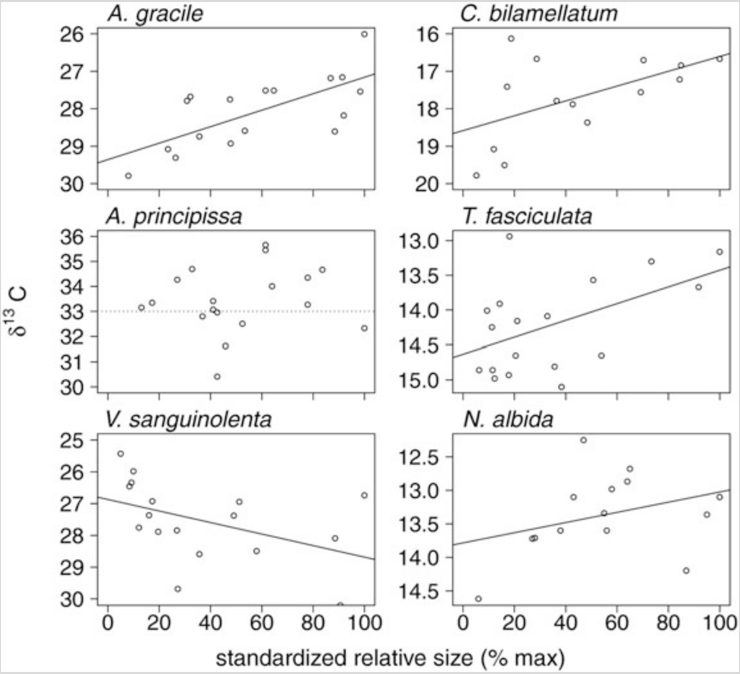
observations (leaf N, photosynthetic capacity) can probably be explained by in situ differences in nutrient acquisition between smaller and larger plants (Zotz et al. 2011), but the mechanisms behind other observations (e.g., stomatal behavior) remain to be elucidated. Most studies on epiphyte ecophysiology in the past did not specify the size of their study organisms, which makes later interpretations difficult. A "demographic approach" to physiological ecology that acknowledges plant size would also be an important step toward bridging the gap between this field of research and population biology (Chap. 6) and community ecology (Chap. 7). Just one example: although the seedling stage is frequently identified as a bottleneck in demographic studies, the ecophysiology of epiphyte seedlings is largely unexplored.

Box 5.1 Size-Related Changes in Foliar $\delta^{13}C$ Values of Vascular Epiphytes (Gerold Schmidt and Gerhard Zotz)

Differences in stomatal aperture (in C_3 plants, Lambers et al. 2008) or different proportions of nocturnal and diurnal CO_2 uptake (in the case of CAM plants, Winter and Holtum 2002) can lead to intraspecific variation in carbon isotope ratios ($\delta^{13}C$) in plants that otherwise grow under identical conditions, e.g., without differences in the isotope composition of the source air. We collected leaf material of 15 species of epiphytes naturally occurring in the moist forest of Barro Colorado Island, Panama. Conspecifics were growing side by side under similar environmental conditions in the same trees. Theoretical considerations lead to the expectation that smaller individuals should be drought stressed more frequently than larger conspecifics, which should result in lower stomatal conductances in C_3 plants and, respectively, a higher reliance on nocturnal CO_2 uptake in CAM plants, both leading to a negative relationship of plant size and $\delta^{13}C$ values. This expectation was fulfilled only to a small degree. Among the 11 tested C_3 species, just three taxa showed the expected pattern (e.g., *Vriesea sanguinolenta*, Fig. 1)—four species (e.g., *Aspasia principissa*) showed no size-related changes and $\delta^{13}C$ values in four other species even became less negative in larger individuals (e.g., *Anthurium gracile*). CAM species showed a more consistent but similarly unexpected pattern. In all four species, $\delta^{13}C$ decreased with plant size, i.e., larger individuals seem to take up a larger proportion of their daily carbon gain at night.

(continued)

Box 5.1 (continued)



The preceding figure shows the size-related changes of foliar $\delta^{13}C$ values in six species of vascular epiphytes. The left column shows C_3 species (*Anthurium gracile*, *Aspasia principissa*, and *Vriesea sanguinolenta*). Additional species (data not shown) with significant increases were *Stelis crescentiicola, Epidendrum nocturnum*, *and Anthurium salvinii*, with no size-related changes: *Christensonella uncata, Guzmania monostachia,* and *Polystachya foliosa*, with decreases: *Dimerandra emarginata* and *Niphidium crassifolium*. The right column shows three CAM species (*Caularthron bilamellatum, Tillandsia fasciculata*, and *Notylia albida*). Data of a fourth CAM species, *Tillandsia bulbosa*, with a similar size-related increase are not shown. Solid lines indicate significant trends (Pearson product moment correlation, $p < 0.05$; the dotted line in the case of *A. principissa* indicates the mean $\delta^{13}C$ value, $p > 0.05$).

A substantial geographical and taxonomic bias in epiphyte ecology at large has already been documented with a bibliometric analysis in Sect. 2.3. This bias is also given in our perception of the physiological ecology of this group. The "typical" study deals with tropical Bromeliaceae—both the state of knowledge of species from the temperate zones and with "unusual" taxa like Ericaceae, Gesneriaceae, etc., let alone, say, Balsaminaceae, are heavily underdeveloped. Thus, generalizations for epiphytes as a group are still quite problematic.

5.1 The Physical Setting

The abiotic conditions encountered by individual epiphytes can hardly be deduced from data of standard meteorological stations. This statement is true for any habitat type in which epiphytes are encountered, but in this chapter I will only focus on the microenvironment of a (tropical) forest. There, steep gradients in light, in moisture, and, less so, in temperature along the vertical axis of a given forest introduce substantial variation in growth conditions of epiphytes (Richards 1996). Noteworthy, these gradients are only temporary during the day. In the case of a lowland forest in Panama (Fig. 5.1), they disappeared by and large during nighttime. Around noon, only c. 20 % light incident on the forest canopy reached the central crowns of trees at 20 m, and just about 6 % the understory (0.5 m), which is more than in many other tropical forests (averaging c. 1–2 %, Richards 1996). These differences did not depend on season. The maximum difference in temperature and relative humidity along the vertical gradient during the 10 documented days was 3.6 °C and 12 %, respectively. Unfortunately, the documentation of such coarse-scale gradients has little predictive power for the microenvironment of any specific growing site in the forest. There is a large number of complicating factors, e.g., differences in the proximity to the forest edge (Davies-Colley et al. 2000), to gaps or streams (Rambo and North 2008), or the position along slopes, i.e., ridge vs. valley (Werner et al. 2012). While all these factors relate to the location of the host in the forest, there are others related to the actual host species or individual, e.g., its architecture or phenology (e.g., evergreen vs. deciduous species, Einzmann et al. 2015; Andrade and Nobel 1997; Manzano et al. 2014). Yet other factors relate to the specific growing site of the epiphyte, e.g., the presence of other vascular or nonvascular epiphytes (Stuntz et al. 2002; Zotz and Vollrath 2003), substrate angle and diameter, and cardinal directions of substrate and epiphyte. Another aspect, which is probably impossible to quantify for practical reasons, are long-term changes in the microenvironment of a particular growing site, i.e., variation in the range of years. Since the longevity of an individual epiphyte can easily be in the range of decades to >100 years (Chap. 6) and local conditions are bound to change because of growth of the host tree and neighboring trees, the documented local conditions experienced by a plant will frequently differ fundamentally from those during earlier establishment.

Microenvironmental measurements are obviously no end in themselves but, e.g., essential prerequisites for the design of meaningful autecological experiments which aim at an understanding of the mechanistic basis behind species distributions. Here we face a common dilemma between the precision of an experiment and its ecological realism (Körner et al. 2005). Even if we focus on only one or a few factors, it is still challenging to connect experiment and reality. Correa and Zotz (2014) discussed this issue for the case of germination studies with

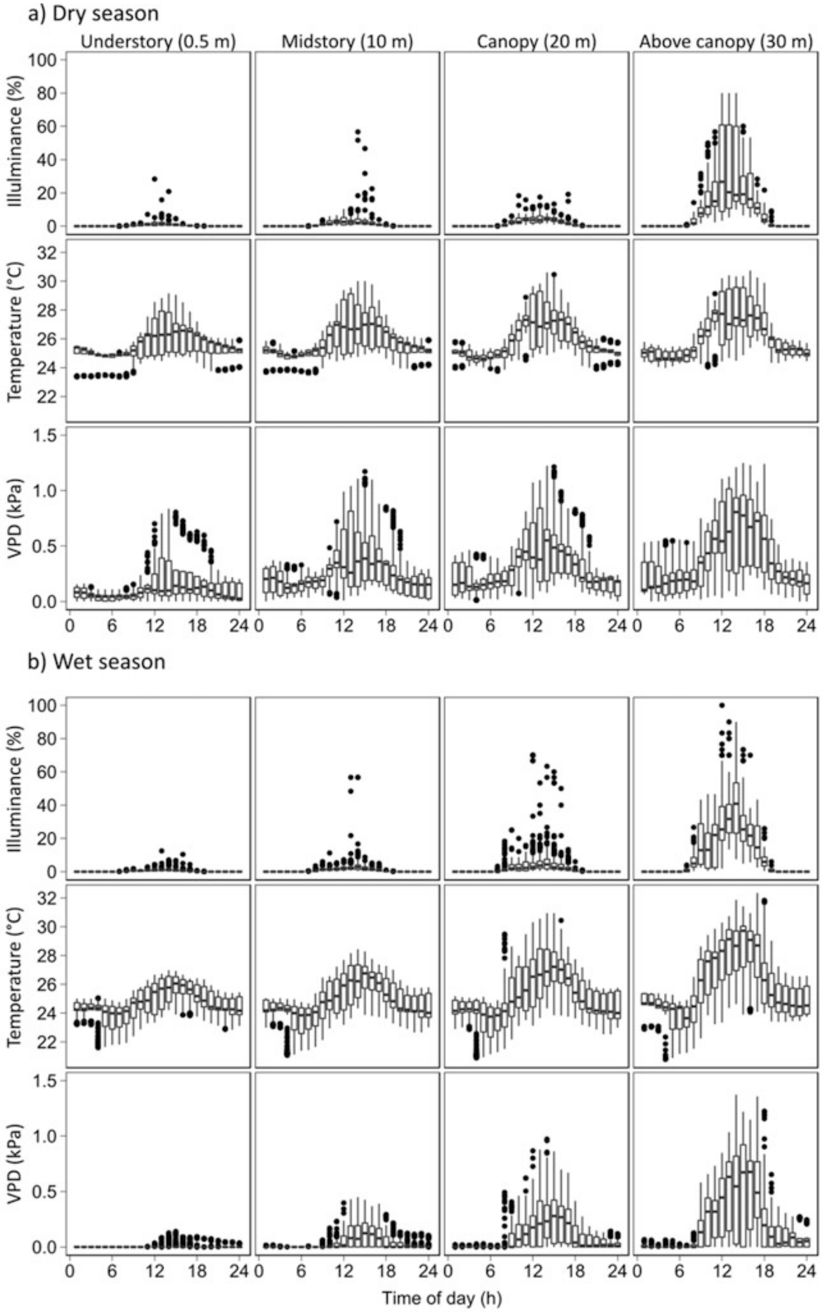


Fig. 5.1 Diel and seasonal variability in microclimatic variables at different height within a tropical lowland forest. Variables are illuminance (as % of the maximum value above the canopy), temperature, and vapor pressure deficit. Measurements were taken every 5 min on 5 days in each season. *Boxplots* are based on hourly means. Modified after Wagner et al. (2013)

epiphytes. A substantial number of germination studies have been published over the last two decades. Many of them studied the temperature responses of germination. Unfortunately, we do not really know how to interpret the results in most cases because we are largely ignorant of the temperature regimes that seeds experience in their natural settings during germination (see Tsutsumi et al. 2011 for an exception). Thus, it is very difficult to relate, e.g., species differences in optimum temperature for germination with observed patterns in species distribution. Clearly, measurements of surface temperatures of the bark of branches and trunks similar to those by Tsutsumi et al. (2011) are necessary. In spite of these rather skeptical statements, the following paragraphs will show that we have made substantial progress in our understanding of the ecophysiology of vascular epiphytes in the quest to link plant characteristics and distributional patterns.

5.2 Plant Water Relations

Water is arguably the most limiting abiotic factor for vascular epiphytes (Gentry and Dodson 1987; Zotz and Hietz 2001). Hence, water relations are treated first. As in plants in general, crucial processes are water uptake, storage, transpiration, and residual, cuticular water loss after stomatal closure.

Relatively little is known about water uptake (e.g., Biebl 1964), although rapid water uptake during and immediately after each rain may be as important for the plant's water balance as are storage and low rates of water loss between rain events (Zotz and Tyree 1996). In many bromeliads, water and nutrients are exclusively taken up by foliar trichomes. A detailed study with *Tillandsia ionantha* identified a bimodal water uptake system in this atmospheric epiphyte (Ohrui et al. 2007). Within a minute, water was taken up by capillary action of the epidermal trichomes, while transfer into leaf tissues took hours. Aquaporins play an important role in the second process, with phosphorylation regulating the activity of these water channels in cell membranes. This regulation seems essential because it restricts water loss during times of drought, while maximizing water uptake during and after rain. Similar processes at cell membranes can be expected in aerial roots, although this has not been studied yet. We do know, however, that the velamen radicum of roots of orchids acts like a sponge: water is absorbed within seconds, but the details of the subsequent uptake into the living cortex are unexplored (Zotz and Winkler 2013).

Besides rainfall, direct precipitation, throughfall, or stem run-off, there are several other potential sources of water for epiphytes that have been discussed in the literature, namely, dew, fog, and atmospheric water vapor as in lichens with green algae (Green and Lange 1994). The physiological consequences of water vapor absorption at high nocturnal humidity have been debated for many years with De Santo et al. (1976) arguing that the uptake of water vapor hydrates living tissues, while Martin and Schmitt (1989) disagreed. Recently, Martin et al. (2013) presented experimental evidence that clearly shows that the absorption of water vapor following increases in atmospheric humidity in atmospheric bromeliads has no physiological relevance for living tissues. Dew, on the other hand, may be quite important for epiphytes in dry forests (Andrade 2003). Direct measurements indicate that the amounts of dew are not sufficient to support growth of the studied bromeliads, but may still be crucial by helping to maintain a favorable water balance during the driest months of the year. Finally, fog may also be an important source of water, particularly in combination with fast winds which reduce boundary layers. Martorell and Ezcurra (2007) proposed that plants have evolved a "narrow-leaf syndrome" to increase the efficiency of fog interception. The so-called tropical lowland cloud forest (Gradstein et al. 2010) with abundant epiphytes probably owes its existence to frequent formations of fog.

Many drought-adapted ground-rooted plants can experience highly negative osmotic potentials (Ψ_π) to promote uptake of strongly bound water from the soil (values in deserts shrubs can be as low as -16 MPa, Larcher 2003). In epiphytes, reported values of Ψ_π are usually less negative than -1.0 MPa (Martin et al. 2004b), which is more in the range of mesophytic terrestrial plants (Gessner 1956; Larcher 2003). At first sight, this may seem puzzling because of the drought-prone growing site of these plants, but—in the absence of soil—water is either abundantly available during short pulses, in which case low Ψ_π is unnecessary to drive water uptake, or practically unavailable even for plants with very negative Ψ_π (Zotz and Hietz 2001).

Autotrophs are bound to open their stomata to take up external CO_2, which inevitably leads to water loss in all but the most exceptional condition. While drought deciduousness is a common observation among trees in seasonally dry habitats, this strategy is relatively rare among epiphytes (e.g., found in many Catasetinae, some *Phalaenopsis* species, and some ferns). The common use of Crassulacean Acid Metabolism (CAM) reduces water loss, as do consistently low stomatal conductance (g_w), and hence transpiration rates, even under favorable conditions (Martin 1994). For example, maximum g_w of eight epiphyte species measured under field conditions in the wet season Venezuela (Griffiths et al. 1989), Panama (Zotz et al. 2001b; Zotz and Tyree 1996), and Trinidad (Griffiths et al. 1986) averaged just 80 mmol m^{-2} s^{-1}, which is less than half the average value of g_w observed in co-occurring trees (Körner 1994). In spite of low g_w the integrated 24-h water loss (T_{24h}) is still substantial when compared to the available water stored in plant tissue [plant water content (PWC)]: Zotz and Tyree (1996) estimated that T_{24h} of a well-watered individual of the bark orchid *Dimerandra emarginata* amounts to almost one-third of PWC. It may take more than a month for stomata to close entirely in epiphytic *Clusia uvitana*, a CAM plant (Fig. 5.2, Zotz and Winter 1996), but even in C_3 species like *Dimerandra emarginata* stomatal closure is postponed for several days. Once stomata are closed, key for survival are the ratio of (1) residual water loss through cuticles and (2) the amount of stored water in relation to the level of dehydration that tissues can survive. The observation of a drastic increase in abscisic acid (ABA) concentrations in epiphyte tissue *after* stomatal closure (Zotz et al. 2001b) may be relevant in this context. The recorded levels (up to 2 nmol ABA $g^{-1}{}_{dw}$ in stems and roots of *Dimerandra emarginata*) are comparable to those in poikilohydric resurrection plants, which

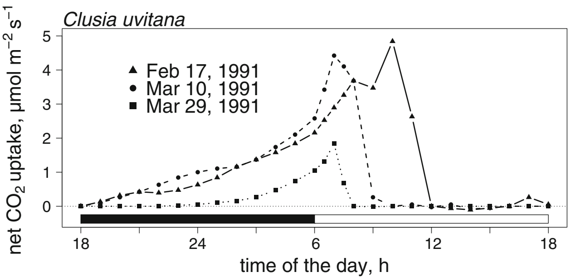


Fig. 5.2 Diel courses of net CO_2 exchange of leaves of an epiphytic C. *uvitana* during the dry season. It had rained only four times since New Year, the last time during the first days of March. *Bars* indicate night and day. Modified after Zotz and Winter (1996)

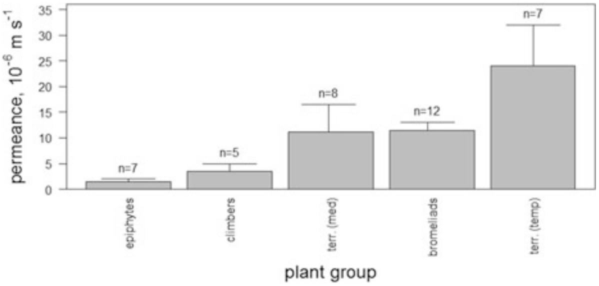


Fig. 5.3 Permeances (P, at 25 °C) for water of cuticular membranes of different plant groups (non-impounding epiphytes, impounding bromeliads, climbers, and (mediterranean and temperate zone) terrestrials. Given are means ±95 % confidence intervals, sample size (*n*) is shown on *top* of the *bars*. After Helbsing et al. (2000) and Benzing (1970, for bromeliads). *Note*: the two studies use different methodologies

suggests a similar function, e.g., in the synthesis of dehydrins and other protective polypeptides.

Data for a limited set of species from a moist tropical lowland forest indicate that permeances of leaf cuticles of non-impounding epiphytes to water vapor are much lower than in other functional groups of plants (Fig. 5.3, Helbsing et al. 2000), but direct measurements of water loss during the first days after stomatal closure still yield daily rates of water loss of 1 to >3 % PWC (e.g., Biebl 1964; Zotz and Tyree 1996; Reyes-García et al. 2012; Kaul 1977). Since some of the xeromorphic species (e.g., *Tillandsia ionantha*, Ohrui et al. 2007) can survive for many months without irrigation, water loss must be substantially reduced during prolonged drought, but actual data on daily rates for extended periods are not available. The amount of water loss that epiphytes can survive is quite impressive. Tissues of *Tillandsia* *fasciculata* could fully recover after water loss of about 60 % of the water present at full turgor (Zotz and Andrade 1998). A congeneric, *Tillandsia ionantha*, did not show irreversible damage until water deficits exceeded 80 % (Benzing and Dahle 1971), while *Guzmania monostachia* recovered after losing over 90 % of the tissue water present at full turgor (Zotz and Andrade 1998). The epiphytic ferns *Niphidium crassifolium* and *Campyloneurum phyllitidis* could even lose about 98 % of PWC and fully recover within 2 days after rewetting (Andrade and Nobel 1997), which resembles the typical response of desiccation-tolerant plants (Bewley and Krochko 1982). A categorization of these plants as poikilohydric is debated, however, in view of the rather stable water potentials (Martin 1994). Although typical for epiphytic mosses and lichens, there are relatively few unambiguous examples of poikilohydry for vascular epiphytes. Most of the alleged or demonstrated cases of desiccation tolerance concern ferns, most prominently Hymenophyllaceae (e.g., Nitta 2006; Cea et al. 2014), but also members of the Polypodiaceae (e.g., *Pleopeltis polypodioides* or *Platycerium* sp., Porembski 2011). Tolerance to dehydration may be even more prevalent among fern gametophytes (Watkins et al. 2007). It could also be a key feature in the rare cases of epiphytic grasses (*Tripogon* sp.) and sedges (*Coleochloa* sp.), but conclusive evidence is lacking (Porembski 2011).

A feature of many bromeliads, only shared with few members of other families (e.g., *Cochliostema odoratissimum*, Commelinaceae), is the existence of an external water and nutrient reservoir formed by overlapping leaf bases. These phytotelmata can hold substantial amounts of water. The record seems to be 20 l in a large *Glomeropitcairnia erectiflora* (Picado 1913). In spite of some claims in the literature that these tanks hold water at all times (e.g., Frank and Curtis 1981; Krügel 1993), direct observations in a moist lowland forest and model calculations suggested otherwise (Zotz and Thomas 1999). Moreover, the effectiveness to bridge rainless periods proved to be strongly size dependent: while large *Vriesea sanguinolenta* plants approach the ideal of a "continuous supply" (sensu Benzing) at least during the rainy season (Fig. 5.4, Schmidt 2000), external water was only available on about 50 % of all days in the smallest tanks. Although qualitatively similar for the dry season, the effectiveness of the tank invariably diminishes. Then, even large plants will rarely be able to rely on a continuous supply of external water. This is a particularly instructive example, why caution is warranted when using the results of ecophysiological studies obtained with larger individuals as explanation for differences in occurrences and spatial distributions of epiphyte species (Zotz et al. 2001a). This limited ability of water-impounding tanks to compensate for intermittent water supply, particularly among smaller individuals, is probably the main reason why tank bromeliads are usually restricted to moister forest formations (Pittendrigh 1948; Benzing 2000; Gilmartin 1983), while in dry forests, they are invariably CAM and are typically found in more exposed sites within the canopy, with better access to rainfall and dew (Graham and Andrade 2004; Reyes-García et al. 2008).

Most of the previous discussion on plant water relations focused on larger individuals, although germination and early establishment are frequent life-history

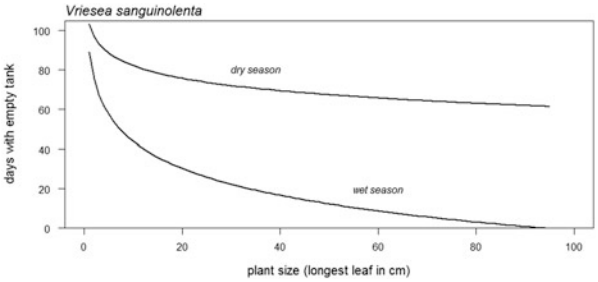


Fig. 5.4 Model predictions of the average number of days with empty tank in *Vriesea sanguinolenta* in lowland Panama as a function of plant size. Climate data for 1991–1999 were used. The dry season lasts c. 120 days and the wet season c. 240 days. Hence, in the smallest individuals the tank can be expected to be empty c. 90 % and 40 % of the time, respectively. Modified after Schmidt (2000)

bottlenecks in plants (Grubb 1977). This bias reflects a paucity of information on the water relations of the early ontogenetic stages of epiphytes. However, what is known is quite impressive and should motivate more studies with additional epiphyte taxa from similar and divergent habitats. For example, during germination xerophytic *Tillandsia flexuosa* show a remarkable tolerance to intermittent desiccation (Bader et al. 2009). A subsequent study (Correa and Zotz 2014) revealed that the germination process in this and other epiphytic bromeliads is only temporarily arrested during short dry periods (12–48 h), but immediately continues after remoistening without hysteresis. Consequently, when expressed as a function of the duration of hydration only (="hydrotime," Black et al. 2006), the frequency and duration of wet–dry cycles had hardly any effect on the germination response (Fig. 5.5). The coma of many bromeliad seeds, which had traditionally been interpreted functionally as related to dispersal and initial anchorage on tree bark, may also play an important role during germination: Wester and Zotz (2011) found that the coma of *Catopsis sessiliflora* promotes germination and early seedling growth by wick-like water uptake. Similarly, the small, gametophytic stage of epiphytic ferns has been similarly overlooked in its ecological importance until recently (Watkins et al. 2007).

To conclude, plant water relations are of critical importance in a habitat that is characterized by highly intermittent supply of moisture, but there are no simple and consistent "evolutionary answers." Relevant traits, at the anatomical, morphological, physiological, and life-history level, vary among species and also within species, e.g., during ontogeny.

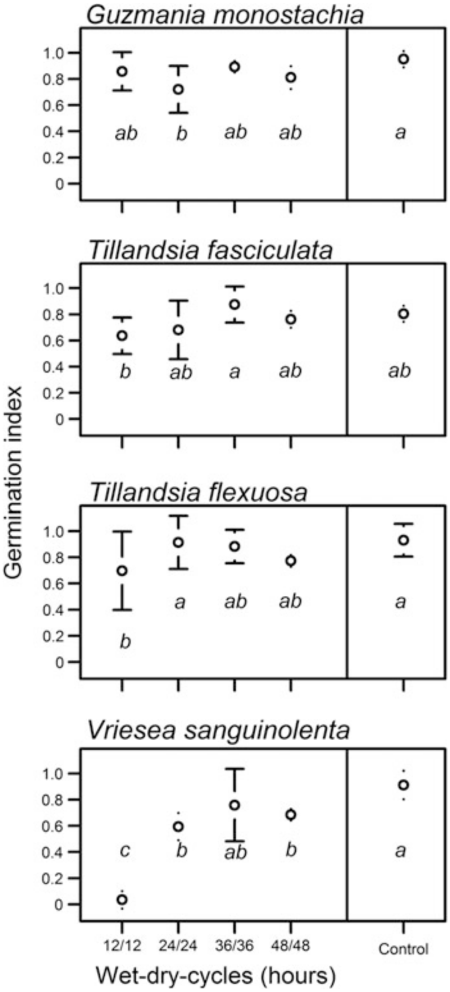


Fig. 5.5 Relationships of the standardized germination index and different wet–dry periods in four bromeliad species (*left panels*) and a control (constantly wet, right panels). Data are means ± SD. Significant differences are indicated by different letters (ANOVA, HSD, $p < 0.05$). Modified after Correa and Zotz (2014)

5.3 Temperature and Plant Function

Apart from moisture, temperature is a major factor determining biological patterns, from the distribution of individual species to the global occurrence of entire biomes. More specifically, temperature may affect establishment, growth, survival, and reproduction of epiphytes from a local scale (shaded and presumably cooler parts of a branch vs. its exposed side), a regional (e.g., reflecting variation due to different elevations), to a global one (e.g., seasonal occurrence of frost). A substantial gradient in microclimatic conditions from the forest floor to the upper canopy of a forest has been documented repeatedly, but the link between physiological requirements of epiphytes and the environment is mostly circumstantial (Wagner et al. 2013; Petter et al. 2016) as is the distinction between the individual effects of the covarying factors radiation, temperature, and humidity. However, a mechanistic understanding of the processes that influence species distributions would be essential to make predictions, e.g., in the context of global change. Figure 5.6 represents an example of an interesting interaction of moisture and temperature in a natural setting, the forests of Killarney National Park in Ireland: because the specific heat of water is very high, moist bryophyte mats on oak trees provide a buffer against mild frost for co-occurring *Polypodium* and *Hymenophyllum* species (Fig. 7.8). Although the air temperature in winter was close to −2 °C for several hours, the rhizomes of these vascular epiphyte species, which grow in these mats, never experienced temperatures below 0 °C.

There is a fair amount of information on temperature responses for horticultural species (e.g., Lootens and Heursel 1998; Guo and Lee 2006), as well as on the basic physiology of individual organs (e.g., Hew et al. 1991). Unfortunately, these studies are only moderately useful to predict comportment in the field. Hence, predictions how, e.g., tropical lowland species will respond to rising temperatures are currently quite speculative (Zotz and Bader 2009). Even predictions of dramatic elevational shifts (Colwell et al. 2008) have not led to a surge in research, but experimental studies would be needed to resolve the issue. For example, available evidence for germination indicates that temperatures of 30 °C or more can actually lead to better germination in some lowland species (Pickens et al. 2003; Pinheiro and Borghetti

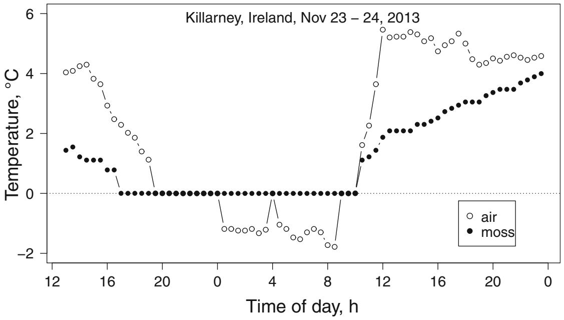


Fig. 5.6 A frost event in the forest of Killarney National Park, Ireland. Shown are both air temperature and the temperature inside a thick moss mat on a horizontal branch of an oak tree, in direct contact with the rhizome of a *Polypodium vulgare* plant. HOBO dataloggers were used

2003). While potentially beneficial for germination, higher temperatures may completely stall subsequent growth as shown in a study with seedlings of *Tillandsia eizii* (Pickens et al. 2003). Growth of the orchid *Erycina pusilla* was similarly affected by culture conditions of 32 °C, which is 5 °C above typical lowland temperatures. Notably, plants growing at these high temperatures did not reproduce (Vaz et al. 2004). This rather erratic account testifies to the fact that relevant information is scarce and generalizations are hardly possible at the moment. Considering that this is an urgent issue, we can only hope that it will receive much more attention in the near future.

The effect of low temperatures has received somewhat more attention, albeit mostly in rather anecdotal form. It is frequently asserted that vascular epiphytes are invariably unable to endure deep frost (Benzing 2012; Nieder and Barthlott 2001), which could serve as an explanation for the upper elevational limit in tropical mountains (e.g., Ibisch et al. 2000) as well as for the observed steep latitudinal gradient in the global occurrence of epiphytes (Chap. 3). Although there is little dissent that most (tropical) epiphytes have indeed a limited tolerance to frost, quantitative evidence is scarce, and, moreover, there are reports of incidences of substantial frost hardiness. For example, quite a few species from low latitudes can survive at least brief periods of subzero temperatures, such as some Mexican *Laelias* (Halbinger 1941) or numerous bromeliads native or cultivated in Florida (Nally 1958; Hall 1958). A pronounced frost tolerance has been documented for species native to the temperate zone: epiphytic individuals of *Polypodium vulgare* can cope with deep frost that lasts for weeks during winter without any visible damage (Fig. 5.7, Zotz 2005). Epiphytic ferns are also found at high elevations, e.g., above 3500 m a.s.l. in the Himalayas, where frost is frequent (Mehra and Vij 1974),

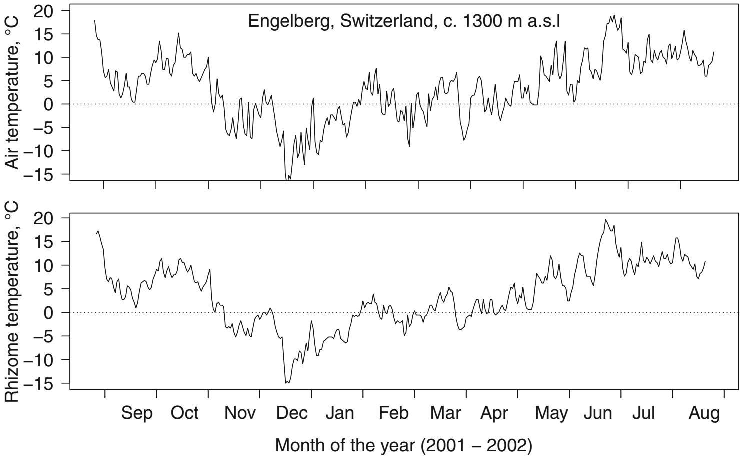


Fig. 5.7 Daily minimum temperature in the immediate vicinity of the rhizome of a *Polypodium vulgare* at c. 5 m height on a moss-covered branch of *Acer pseudoplatanus* in the Swiss Alps at Engelberg (c. 1300 m a.s.l.) and immediately adjacent air, determined with two tidbit data loggers between 25 Aug 2001 and 14 Aug 2002 (Zotz, unpubl. data)

and at high latitudes (Puyehue, 41° S), where a few ferns like *Grammitis magellanica* are growing at the tree line with severe frost during winter (Alfredo Saldaña and Gerhard Zotz, unpubl. obs.). This provides additional, albeit indirect, evidence that epiphytes are not invariably characterized by low frost tolerance. The exact mechanisms behind both the latitudinal and the elevational distributional limit of vascular epiphytes are thus still open research questions.

5.4 Mineral Nutrition

More than two decades ago, David Benzing complained the lack of data on nutrition in vascular epiphytes (Benzing 1990). Our current knowledge is still not even remotely comparable to that of nutrition in ground-rooted plants, but substantial progress has been made. This positive statement is based on studies at the level of individual organs, entire plants up to that of entire forests. For example, the uptake kinetics of the major elements N, P, K have been characterized in detail in epiphytic bromeliads and orchids (e.g., Inselsbacher et al. 2007; Winkler and Zotz 2010), direct uptake of alternative nitrogen sources such as amino acids or urea via roots or absorbing scales has been demonstrated (e.g., Trepanier et al. 2009), nutrient fluxes within individuals for vegetative and reproductive function have been quantified (e.g., Zotz and Richter 2006), and the atmospheric input into canopies (Hietz et al. 2002; Clark et al. 1998) or the effect of large-scale fertilization on entire epiphyte communities has been studied (e.g., Benner and Vitousek 2007), as have been nutrient relationships of epiphytes along large elevational gradients (Cardelús and Mack 2010; Wegner et al. 2003).

Benzing coined the terms “continuous supply” vs. “pulse supply” (Benzing 1990), which are useful as long as they are not understood as a dichotomy but as endpoints of a gradient of temporal water and nutrient variability. Tank bromeliads in wet forests or any epiphyte rooting in thick mats of dead organic material in a montane forest, hardly differing from a ground-rooted plant, exemplify one extreme, while non-impounding twig epiphytes in dry or moist forests (or atmospheric bromeliads on electrical wires, Fig. 1.2a) with usually brief and intermittent supply of both water and nutrients the other. Arguably, most epiphytes function somewhere in between these extremes.

In the following, I will treat important aspects of the nutrient relations of vascular epiphytes, covering the supply side, the demand, and the pools. Nutrient pools and fluxes from an ecosystem perspective will be treated later (Sect. 9.3).

5.4.1 Nutrients in the Forest Canopy

The nutrient regime in forest canopies is influenced by both external and internal inputs (Fig. 9.2). External sources encompass dry deposition and precipitation, but also the deposition of nutrients in non-precipitating droplets in clouds or fog (also called “occult” or “horizontal” precipitation, Reynolds and Hunter 2004). Internal sources encompass the leachates of nutrients from host-tree foliage and liberation of nutrients due to the decomposition of woody components or the decay of leaf litter. Yet another "internal" source is represented by N_2-fixing, free-living, or symbiotic diazotrophs (Fürnkranz et al. 2008).

Fine litter components may be intercepted by branches, epiphytes, or fungal litter-trapping systems (Nadkarni and Matelson 1991; Snaddon et al. 2012). When litter deposition rates on branches exceed decomposition rate, organic material can accumulate and canopy soils form. Such soils lead to fundamental changes in the growth conditions of epiphytes. While the nutrient supply of bark epiphytes relies on low nutrient levels from atmospheric deposition and relatively enriched stemflow (Table 5.1, Chuyong et al. 2004; Veneklaas 1990; Awasthi et al. 1995), concentrations of nutrients in canopy soils (and the detritus in bromeliad tanks) are often higher than those on the forest floor (Table 5.2). Similarly high nutrient levels

Table 5.1 Nutrient concentrations in stemflow measured in various temperate, subtropical, and tropical forests

Nutrient elements						Site	Tree specifications	Source
Na	Ca	Mg	K	N	P			
0.60	3.04	0.52	0.25	0.76	0.02	Florida, USA	*Taxodium distichum* (dwarf)	Benzing and Renfrow (1974b)
0.60	9.60	0.60	1.30	0.40	0.02	Florida, USA	*Taxodium distichum* (vigorous)	Benzing and Renfrow (1974b)
–	0.52	0.13	0.29	0.04	0.03	Rainforest, Cameroon	Various	Chuyong et al. (2004)
–	–	–	–	3.49	0.18	Subtropical forest, Himalaya	Unspecified	Awasthi et al. (1995)
3.00	1.00	4.30	3.00	1.30	0.10	Cloud forest, Haiti	*Eugenia jambos*	Curtis (1946)
8.00	4.95	4.20	7.10	0.05	–	Tropical montane, Australia	*Ceratopetalum virchowii*	Herwitz (1991)
2.15	0.35	0.70	0.60	0.05	–	Tropical montane, Australia	*Balanops australiana*	Herwitz (1991)
1.90	0.02	0.30	0.80	0.07	–	Tropical montane, Australia	*Elaeocarpus foveolatus*	Herwitz (1991)
0.62	1.10	0.16	1.07	0.04	–	Temperate rainforest, Chile	*Nothofagus betuloides*	Oyarzun et al. (2004)

– not determined

Data are means in mg L^{-1}. Note that there is huge variation related to tree species exceeding up to two orders of magnitude within a site (Herwitz 1991) as well as large intraspecific variation between conspecifics differing in vigor (Benzing and Renfrow 1974b)

Table 5.2 Nitrogen, phosphorus, and potassium concentrations of canopy soils and animal-derived substrates, Sampling methods varied, but "canopy soil" or "fine earth" generally refers to the heavily decomposed fraction with no or few recognizable plant remains

Country	Vegetation type	N %	P %	K %	Comments	Source
China	Montane cloud forest	2.0	0.09	0.022	Canopy humus	Chen et al. (2010)
Colombia	Humid montane forest	1.4	0.12	0.03	Fine earth on trunk foot <3 m	Hofstede et al. (1993)
		1.1	0.07	0.05	Fine earth on basal 1/3 of large branches	
Costa Rica	Humid montane forest	2.2	–	–	Canopy soil	Vance and Nadkarni (1990)
		1.4	–	–	*Terrestrial H horizon*	
		1.0	–	–	*Terrestrial A1 horizon*	
Costa Rica	Lowland forest	2.0	–	–	Canopy soil	Wania et al. (2002)
		0.5	–	–	*Terrestrial soil*	
Costa Rica	Lowland forest	2.4	–	–	Canopy soil	Cardelús et al. (2009)
Costa Rica	Montane forest, 2900 m	1.8	–	0.1	Canopy soil	Hertel and Köhler (2010)
		1.8	–	*0.2*	*Terrestrial soil*	
Ecuador	Wet forest	2.9	0.40	0.8	Ant garden carton	Benzing (1990)
El Salvador	Six humid montane forests 1950–2280 m	1.7	0.20	–	Canopy soil < 2 mm fraction	Klinge (1963)
	Three pine-oak forests 1000–2100 m	1.3	0.20	–	<2 mm fraction	
Florida, USA	Swamp forest	1.9	0.11	–	In bromeliad tank	Benzing (1980)
New Guinea	Lowland rainforest	1.5	0.06	0.19	Canopy soil	Grubb and Edwards (1982)
Panama	Moist lowland forest	2.1	0.14	–	In bromeliad tank	Zotz and Hietz (2001)
		0.5	*0.07*	–	*Terrestrial A1 horizon*	
Taiwan	Subtropical forest	1.9	0.14	0.28	*Asplenium nidus*	Yang et al. (2001)
		1.8	0.17	0.21	*Pseudodrynaria coronans*	

(continued)

Table 5.2 (continued)

Country	Vegetation type	N %	P %	K %	Comments	Source
Togo	Humid montane forest	2.5	0.35	–	<2 mm fraction	Klinge (1963)
Venezuela	Seasonally inundated savanna	0.8	0.03	3 meq 100 g^{-1}	Behind palm leaf base	Putz and Holbrook (1989)
		0.3	*0.03*	*0.5 meq 100* g^{-1}	*Terrestrial soil*	
Venezuela	Two humid montane forests	2.2	0.23	2.4	Canopy soil	Rabatin et al. (1993)
		0.6	*0.13*	*0.76*	*Terrestrial soil*	
Venezuela	Lowland forest	2.7	0.21	0.95	Ant garden carton	Blüthgen et al. (2001)
		0.8	0.05	0.25	Termite nest	

– not determined
When available, comparative data for terrestrial soils are also shown (*in italics*)

can be found in substrates constructed by animals, e.g., in ant gardens (Table 5.2, Blüthgen et al. 2001). The actual availability of these nutrients for epiphytes does not directly follow from such values, but several studies show that mineralization rates in the canopy are similar or even faster than in the mineral soils of the forest floor (Cardelús et al. 2009; Pérez et al. 2005; Vance and Nadkarni 1990). However, a major difference between forest and canopy soil is the low rate of nitrification in the latter, a fact already stressed by Harbrecht (1941). Without doubt, the uptake efficiency of roots and absorbing scales (in bromeliads) is a key issue to assure that ions in solutions can be scavenged before they are lost with stemflow.

Tree canopies offer a heterogeneous spatial and temporal mosaic of nutrient sources and nutrient levels, but there are some patterns with predictive value (Wania et al. 2002). For example, the relative availability of internal and external sources depends on the position in the vertical gradient from canopy edge to forest soil. In the periphery, epiphytes (almost) completely depend upon atmospheric sources, while lower strata will increasingly profit from leachates and the wash-off of dry deposited aerosols and gaseous materials from leaves and branches. Studies with stable isotopes have provided evidence of the differences in nutritional modes with canopy position (Hietz et al. 2002; Wania et al. 2002). At a smaller spatial scale, accumulation of leaf litter in large *Asplenium nidus* results in substantial enrichment of the concentrations of N and K in stemflow below these ferns (Turner et al. 2007). In the New World, bromeliad tanks can be expected to have a similar effect on their immediate environment. Whether this local enrichment is strong enough to stimulate increased growth of other epiphytes, algae, and fungi on the trunk below such litter-impounding plants, as suggested by Turner et al. (2007), remains to be shown. Animal-derived structures, e.g., ant carton nests, represent another type of nutrient hotspot (Table 5.2), particularly in regard to P and K concentrations, and *Peperomia* species growing in these ant gardens can have remarkably high concentrations of these macronutrients (Fig. 5.10).

Temporal variation in the nutrient concentrations of canopy fluids is also substantial. During an individual rainstorm, initial nutrient concentrations in the stemflow are relatively high, primarily due to wash-off of dry deposition, exponentially decaying to a steady input, which is primarily fed by leaching (Levia et al. 2011). It has been argued that the velamen radicum, typical for epiphytic orchids, is capable of capturing these nutrient peaks (Went 1940). Recent evidence supports this notion (Zotz and Winkler 2013).

Nutrient input can also be highly punctuated at a larger timescale. More than 50 % of the total annual wet deposition of Ca, K, Mg, P, N to a dry forest in Honduras occurred within 1–10 days (Kellman et al. 1982). It is unclear how representative this study is for other forests, but the published observations on both the short-term dynamics and the annual dynamics of nutrients in the forest canopy justify the expectation that epiphytes are strongly selected for the ability to absorb these irregular pulses of atmospheric nutrients.

5.4.2 Nutrient Uptake

Although nutrient uptake in epiphytes has been studied for more than a century (Haberlandt 1914), exact characterizations of the uptake kinetics of major ions into roots and scales of, respectively, epiphytic orchids and bromeliads have not been reported until very recently (Inselsbacher et al. 2007; Winkler and Zotz 2009, 2010; Zotz and Winkler 2013). One interesting finding was that absorbing scales show biphasic uptake kinetics (Fig. 5.8).

The presence of a low-affinity and a high-affinity system allows these bromeliads to take up ions effectively from both highly diluted and rather

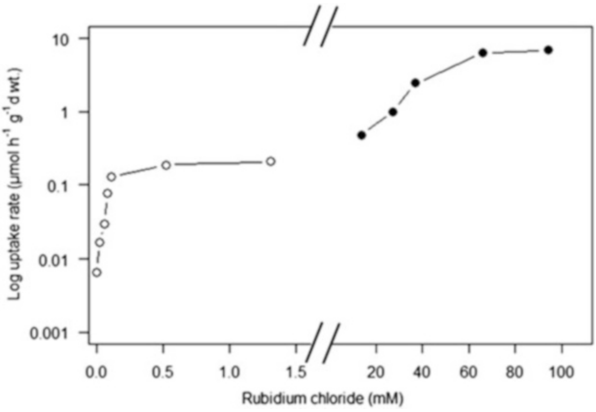


Fig. 5.8 Biphasic uptake kinetics of foliar trichomes of tank bromeliads for rubidium, which was used as potassium analogue in the study of Winkler and Zotz (2010) with *Vriesea* "Splenriet". High-affinity uptake (*open symbols*) was ATP dependent, while low-affinity uptake (*closed symbols*) was reduced by known inhibitors of potassium channels. Modified after Winkler and Zotz (2010)

concentrated solutions. Low nutrient concentrations are probably more typical in situ, but the ability to take advantage of the occasional yet ephemeral high nutrient source (e.g., feces or decaying fruits) may be essential. Feedback of physiological characteristics to environmental conditions can be expected, similar to fine roots of terrestrial plants (Bucher 2007). There, uptake characteristics are modified through changes in transporter abundance and substrate affinity of membrane transporters. Whether the response of uptake organs of epiphytes (roots, bromeliad trichomes) is comparable or exceptional in terms of magnitude and speed remains to be shown.

Consequently, one would also expect considerable intraspecific variation in uptake rates, particularly in heteroblastic bromeliads (see Chap. 4), in which small "atmospheric" plants lack a tank and are "pulse supplied" compared to larger, more "continuously supplied" conspecifics with tanks. Indeed, uptake rates for phosphorus and rubidium, used as an analogue to potassium, decreased substantially from smallest to largest plant in both *Vriesea sanguinolenta* and *Vriesea heliconioides* (Meisner et al. 2013).

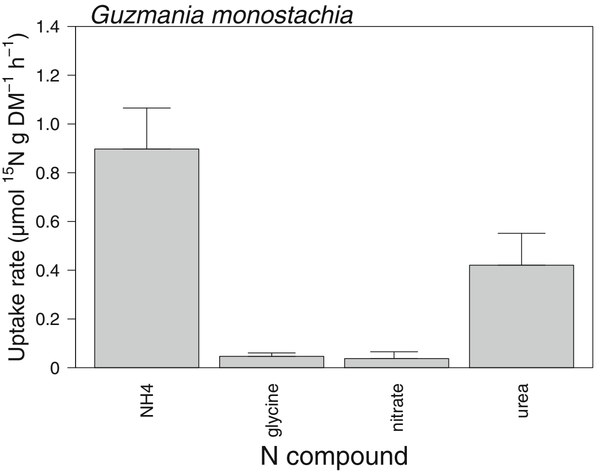
The role of roots in tank bromeliads of Benzing's type III and IV (compare Table 4.1) in nutrient uptake is far from understood and experimental results are contradictory. While nutrient uptake rates of roots were comparable to those of leaves in large individuals of *Guzmania monostachia* (S. Reisinger, A. Richter, W. Wanek, P. Hietz, and A. Reich, unpubl. res.) or in juveniles of *Vriesea sanguinolenta* (K. Wilhelm and U. Winkler, unpubl. res.), other studies with greenhouse-grown *Aechmea* sp. (Winkler and Zotz 2009) or *Guzmania lingulata* plants (Nadkarni and Primack 1989) failed to detect any radicular uptake. Demonstration of radicular capacity for nutrient uptake in tank bromeliads is not necessarily equivalent to an important role under natural conditions. Field experiments determining fluxes are needed to shed light on this issue. These will have to consider the complicating role of diverse environmental conditions and ontogenetic changes (Petit et al. 2014, compare also Sect. 4.6 on claims on the occurrence of velamina in bromeliad roots).

In general, nutrient uptake does not seem to be restricted to inorganic forms. There is evidence that both bromeliads (Endres and Mercier 2003; Inselsbacher et al. 2007) and orchids (Trepanier et al. 2009) can take up alternative nitrogen sources such as amino acids or urea via roots or absorbing scales (Fig. 5.9). However, up to now we cannot put such observations in an ecological context. To judge the importance of these physiological characteristics for growth and reproduction of naturally growing plants, we would need data on the relative availability of different N-species in the rooting zones or the tank of epiphytic plants and conduct pertinent experiments. A similarly unresolved question is variability of uptake kinetics in time, e.g., in dry and wet seasons.

5.4.3 Nutrient Concentrations in Tissue of Vascular Epiphytes

A thorough review of the literature and unpublished data from various sources (see Acknowledgments) yielded more than 2000 data points for more than 600 species

Fig. 5.9 Foliar uptake rates of ^{15}N of field-grown *Guzmania monostachia* plants. Data are means ± standard error (SE; $n = 3$). Tested N compounds were ammonium (NH_4^+), nitrate, glycine, and urea. Sabine Reisinger, Andreas Richter, Wolfgang Wanek, Peter Hietz und Alexandra Reich, unpubl. data



in 34 families of epiphytes and hemiepiphytes (of which only epiphytic individuals were included). Most information is available for leaf nitrogen (N, c. 40 % of all data points) and leaf phosphorus (P, c. 15 %), but scattered information is available even for micronutrients such as copper (Cu), molybdenum (Mo), or boron (B). Considering the different forest types, varying analysis methods, and very uneven sample sizes of different taxa, generalizations should be done with caution (Fig. 5.10), but a number of trends can be deduced. First, nutrient concentrations are relatively low compared to the minimum requirements for eutrophic vegetation (Marschner and Marschner 2012), but individual plants can deviate substantially from this trend. Particularly remarkable are reports of very high nitrogen concentrations in a few orchids (>4 %, e.g., Benzing 1978; Wester et al. 2011) and of c. 10 % K (potassium) in an unidentified *Peperomia* species growing in an ant garden (Blüthgen et al. 2001). Second, in spite of considerable variation within families in all elements, Bromeliaceae and Ericaceae show quite consistently the lowest nutrient concentrations, while those in aroids are usually highest. This agrees with the results of earlier comparative studies that reported similar rankings (Wester et al. 2011; Stuntz and Zotz 2001). The low levels of N in Ericaceae are particularly puzzling. Several studies have focused on epiphytic family members and detected ericoid mycorrhizae, which can typically use complex organic sources of N and P (e.g., Bermudes and Benzing 1989; Rains et al. 2003). Thus, one could actually expect relatively high N concentrations in Ericaceae compared to other epiphytic taxa.

These numbers do not allow an answer to the question which element is most limiting for vascular epiphytes. Generally, P is most limiting in tropical forests on weathered soil (Vitousek 1984), and the results of a number of studies with epiphytes indeed point to P limitation rather than N limitation (Zotz 2004b; Zotz

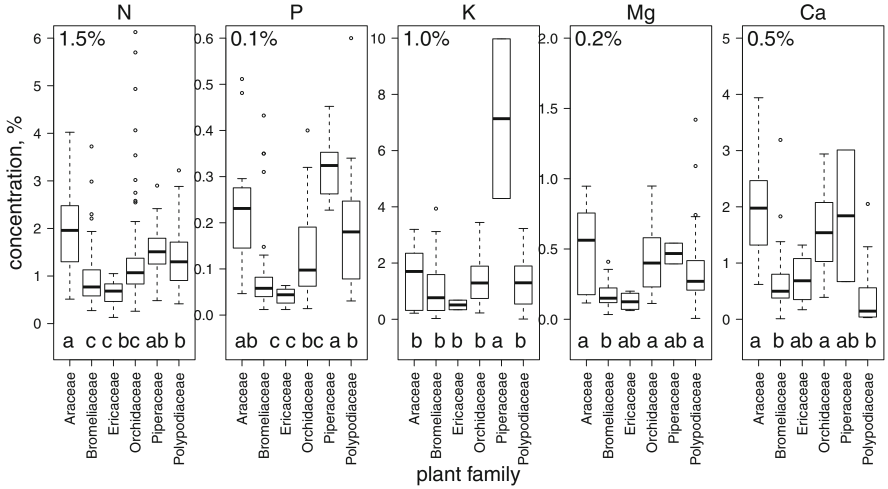


Fig. 5.10 Nutrient concentrations in % dry mass in leaves of epiphytes. Families with at least two data points for each of the five elements were considered (range from 230 samples: N in orchids to 2: K in Piperaceae). Only data from nonreproductive, field-grown material (mostly leaves, a few times entire shoots) on a dry mass basis were included. Generalized minimum requirements for eutrophic vegetation (Marschner and Marschner 2012) are given for each element in the *upper left corner*. Different letters below each *box* indicate significant family differences (one-way ANOVA, Tukey HSD, $p < 0.05$). Data from many sources

and Richter 2006; Cardelús et al. 2009; Cardelús and Mack 2010). Although suggestive, none of these studies provides unequivocal evidence. This is also true for an experiment in which N and P supply were varied in a full factorial design with field-collected plants of three bromeliad species (Zotz and Asshoff 2010). On the one hand, fertilization did not lead to higher tissue concentrations of N compared to natural levels, while tissue P concentration increased up to sevenfold. On the other hand, both N and P supply had a significant effect on relative growth rate (RGR). Noteworthy, even the lowest P fertilization level led to a decreased N:P ratio. These results are compatible with the notion of co-limitation by N and P and of particularly severe shortage of P supply under natural conditions.

The latest contribution that focuses on this question (Wanek and Zotz 2011) used an approach based on theory which predicts that N-limited plants will reflect the natural ^{15}N abundance of their N sources, while P-limited plants fractionate against ^{15}N (Evans 2001). Both experimental and field-grown plants of *Vriesea sanguinolenta* showed significant fractionation, which is the first unambiguous evidence for P-limitation under field conditions.

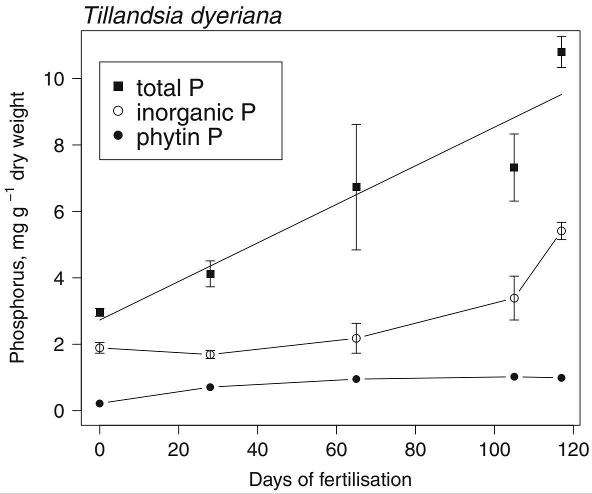
Without experimental studies, we can hardly come to unambiguous conclusions how nutrient-limited vascular epiphytes really are in situ. First, even the relatively low nutrient concentrations observed in many cases (Fig. 5.10) do not necessarily indicate in situ nutrient limitation. Although a positive effect of fertilization on plant nutrient status and growth has been demonstrated experimentally for selected species (e.g., Benzing and Renfrow 1974a), other factors, particularly water shortage, may be of overruling importance in the field, which is suggested by studies that varied both nutrient and water supply simultaneously (Laube and Zotz 2003; Zotz et al. 2010). However, relatively high concentrations of particular nutrient elements may reflect luxury consumption rather than high levels of metabolically active compounds. Luxury consumption is typical for nutrient-poor habitats (Chapin 1980). If phosphorus is indeed most limiting, one would expect luxury consumption to be most prominent in this element. Indeed, there is evidence for this to be true (Zotz and Asshoff 2010). Phosphorus that is not immediately needed in current metabolism can be stored as vacuolar phosphate, as polyphosphate, or as phytic acid (myo-inositol-1,2,3,4,5,6-hexakisphosphate or InsP6). Most research on phytic acid has focused on its occurrence in seeds, where it usually constitutes >70 % of total phosphorus (Raboy 2009). In actively growing green tissue, phytic acid usually plays a minor role (Alkarawi and Zotz 2014). A study by Winkler and Zotz (2009) seemed to be at odds with this general conclusion because autoradiograms of leaf tissue *of Aechmea fasciata* plants, which had been fed with radioactive [^{32}P]phosphoric acid, suggested that free soluble inorganic phosphate was largely converted to phytic acid. However, later experiments (Box 5.2) provide clear evidence for another epiphytic bromeliad that P is primarily stored as inorganic P rather than as phytic acid.

Box 5.2 Luxury Consumption in Epiphytic Bromeliads (Uwe Winkler and Gerhard Zotz)

Luxury consumption, i.e. the uptake of nutrients in excess of current metabolic needs is typical for nutrient-poor habitats (Chapin 1980). Since P is arguably the most limiting mineral element in vascular epiphytes (Wanek and Zotz 2011), we focused on the changes in the concentrations of phytic acid and inorganic phosphate as two potential storage compounds of P during a four month fertilization experiment with *Tillandsia dyeriana*. All plants were initially about 10 cm high, with 10–14 leaves and a tank volume of approx. 1 mL. They were kept in the greenhouse at c. 26 °C, at a relative humidity of c. 60 % and a light dark regime of c. 12:12 h. The plants, which came from a commercial nursery (Corn. Bak B.V., Asseldelft, The Netherlands), had very high initial P concentrations and had thus to be nutrient-starved first for 6 months by only irrigating them with distilled water every other day. Then, maintaining this irrigation scheme, plants received a fertilizer solution once a week, which contained 9 mM N as ammonium nitrate and 3 mM P as

(continued)

Box 5.2 (continued)
phosphate. Entire plants were collected in regular intervals and total P, phytin acid-P and inorganic P were determined as described in Alkarawi and Zotz (2014).



The preceding figure shows means of 3 replicates and standard deviations are given whenever larger than symbol size. Clearly, most of the initial foliar P-concentration of c. 3 mg g_{DW}^{-1} was present in the form of inorganic phosphate (P_i, $> 60\,\%$), exceeding the proportion of P in phytic acid by almost one order of magnitude. There was a steep increase in phytic acid concentrations in the first month of the fertilization experiment, which also led to a proportional change (17 % of total P in the form of phytic acid-P vs. 41 % in P_i). The increase in phytic acid continued for another month and leveled off afterwards, while Pi continued to increase for the entire 4 months. The relative changes in phytic acid concentrations exceeded those of both total P and P_i, but in absolute terms inorganic phosphate increased four-fold more.

In conclusion, although phytic acid acts as a storage compound in green tissue of this epiphytic bromeliad, particularly in the early stages of recovery after nutrient deprivation, inorganic P is clearly the primary storage compound during luxury consumption.

5.4.4 Reproductive Investment

Reproductive allocation is generally defined as the proportion of resources, e.g., biomass or nutrients, which are invested in reproductive organs or parts thereof, e.g., seeds (Bazzaz 1996). Since most epiphytes face both frequent disturbance and high abiotic stress (sensu Grime 1977), epiphytes are expected to allocate a large proportion of their resource pools to support fecundity (Benzing 1990). Indeed, published data indicate that up to 30 % of total plant biomass is invested in reproductive structures (Benzing and Davidson 1979; Benzing and Ott 1981; Zotz 1999). Table 5.3 lists published details for two species of orchids and two species of bromeliads along with unpublished data from nine species of orchids from Barro Colorado Island, Panama (G. Zotz, unpubl.).

A particularly noteworthy observation is the enrichment of phosphorus in fruit of *Aspasia principissa* by a factor of two with concentrations of almost 2 mg P g^{-1} dry mass. Since the capsules account for about one-fourth of the total biomass of an individual plant in this species, a single large fruit thus contains almost as much P as all remaining plant parts together (Table 5.3). High nutrient allocation was also found in the case of K, while N and Mg scaled approximately with fruit biomass in this and other orchids. The data for bromeliads are too few to merit a detailed discussion at the moment. Overall, the documented values for 13 species of epiphytes exceed the reproductive investment in the majority of terrestrial perennials and approach a level similar to that in many annuals (Hancock and Pritts 1987).

The shown data document substantial intraspecific variation. One possible source of such variation is plant size, since reproductive allocation in plants is frequently size dependent (Samson and Werk 1986). To date, there is a single study addressing this question in vascular epiphytes. Surprisingly, reproductive allocation in the orchid *Dimerandra emarginata* (expressed as relative investment of biomass or nutrient elements such as N, P, K) did not vary with size (Zotz 2000). However, while the investment during a given reproductive event was similar in smaller and larger individuals, the frequency of reproduction varied substantially. Plants >25 cm reproduce every year, while smaller individuals show an increasingly lower probability (Zotz 1998): there is a 60-fold increase in the average *annual* investment into fruits from smallest to largest reproductive individual.

Model calculations for pools and fluxes of the major elements P and N in mature individuals of the tank bromeliad *Vriesea sanguinolenta* indicate that reproduction is primarily limited by P-supply (Fig. 5.11, Zotz and Richter 2006). The data suggest that the supply is so low that it takes two years to replenish P-pools to allow renewed reproduction. It is probably not mere coincidence that 2 years is the most commonly found interval between reproduction events in this epiphyte (Zotz et al. 2005).

Table 5.3 Reproductive allocation (% resource in capsule compared to resource in entire plant) in nine epiphytic orchids and two epiphytic bromeliads

Species	Biomass	N	P	K	Mg	Source
Aspasia principissa	25.8	28.6	48	37.1	22.1	Zotz, unpubl
Brassavola nodosa	11.1 ± 6.3	13.7 ± 8	19.8 ± 11.5	28.1 ± 7.2	13.6 ± 5	Zotz, unpubl
Camaridium ochroleucum	8.7 ± 3.3	5.3 ± 2.5	6.9 ± 2.5	17 ± 10.5	8.8 ± 5.4	Zotz, unpubl
Catasetum viridiflavum	6.6	9.8	19.4	29.4	8.8	Zotz, unpubl
Caularthron bilamellatum	8.8 ± 1.4	8.4 ± 3.9	6.7 ± 4	10 ± 2.9	5.5 ± 1.4	Zotz, unpubl
Dimerandra emarginata	12.9 ± 4.2	11.7 ± 5.3	17.6 ± 7.0	30.7 ± 12.4	12.0 ± 6.3	(Zotz 1999)
Encyclia tampensis	–	26.3 ± 8.4	25.7 ± 6.9	31.9 ± 14.2	16.2 ± 6.7	Benzing and Ott (1981)
Epidendrum difforme	20.3 ± 11.1	16.8 ± 7.1	25.8 ± 11.2	42.2 ± 17.2	23.9 ± 9.8	Zotz, unpubl
Epidendrum nocturnum	13.4 ± 5.4	23.7 ± 7.7	36.4 ± 7.1	35.6 ± 3.2	23.2 ± 6.3	Zotz, unpubl
Specklinia brighamii	6.2 ± 3.4	9.2 ± 5.7	11.5 ± 7.3	10.1 ± 6.2	7.8 ± 4.2	Zotz, unpubl
Sobralia bletiae	5.6	3.6	3.9	7.5	3.7	Zotz, unpubl
Orchids—Averages	11.9 ± 6.6	14.3 ± 8.5	20.2 ± 13.4	25.4 ± 12.2	13.2 ± 7.2	
Tillandsia streptophylla	10.5 ± 4.5	22.8 ± 8.0	20.4 ± 6.9	13 ± 3.0	9.0 ± 3.8	Benzing and Davidson (1979)
Vriesea sanguinolenta	6	21	37	8	4.5	Zotz and Richter (2006)
Bromeliads—Averages	8.3	21.9	28.7	10.5	6.8	

Data are means ± SD ($n = 3–4$ individuals) or means of two samples

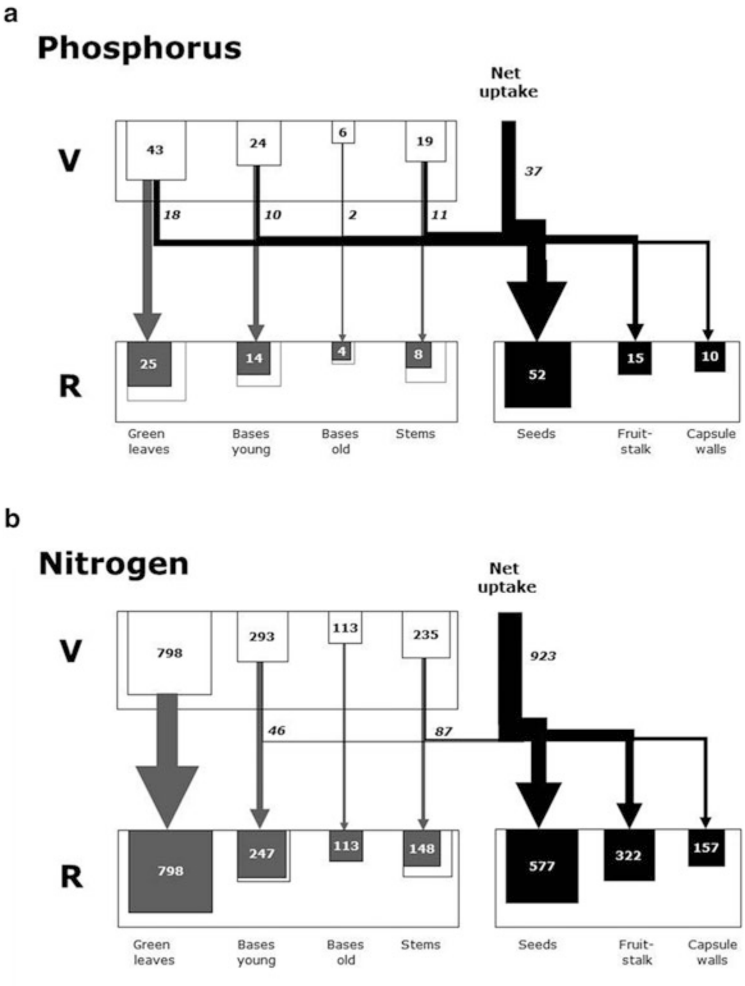


Fig. 5.11 Nutrient pools (*bold*) and fluxes (*italics*) during the vegetative (*V*) and the reproductive state (*R*) of an epiphytic bromeliad *Boxes* represent different compartments of *Vriesea sanguinolenta* plants. Figures in each *square* are nutrient contents in mg plant^{-1}. Fluxes are estimated from the different P or N pools in the vegetative compartments during the vegetative and the reproductive state. Data were collected over 24 months. Net uptake was estimated as the difference of the nutrient content of reproductive organs and the sum of all fluxes from vegetative compartments. Reproduced with permission from Zotz and Richter (2006)

5.4.5 Associations with Fungi and Cyanobacteria

For ground-rooted plants, the importance of mycorrhizae for plant nutrient supply has been demonstrated for a long time (e.g., Alexander et al. 1984). For epiphytes, there are an increasing number of reports on the occurrence of mycorrhizae (Chap. 8), but very little information on the functional implications. One of the few exceptions is a study by Wu et al. (2011), who report that orchid mycorrhizal fungi in *Phalaenopsis* roots significantly increased plant growth. The mechanism behind this observation was not investigated. More conclusions can be drawn from another study in which lithophytic *Lepanthes rupestris* was treated with fungicides (Bayman et al. 2002). One fungicide which reduced the frequency of both pelotons and fungi in roots of *Lepanthes rupestris* seedlings and juveniles increased mortality, whereas the fungicide that decreased the frequency of fungi in leaves, without affecting pelotons, did not. These findings are consistent with a positive role for mycorrhizae and a negative role for pathogens and/or endophytes. There is also the suggestion that saprobic ascomycetes associated with the velamen of orchids may indirectly improve nutrient access by decomposing the substrate outside the roots (Herrera et al. 2010). Taken together, information on the functional role of fungal associates is scarce and does currently not really suggest a very prominent role for nutrient uptake in epiphytes, not least because of the low frequency of mycorrhizae among epiphytes. However, in view of the accumulating evidence of an important role of the diverse groups of fungal symbionts (mycorrhizal fungi, leaf endophytes, and dark septate endophytes) for plant functioning in general (Kivlin et al. 2013), it is certainly worthwhile to have another look at the relevance of the epiphyte-fungal relationship (Chap. 8).

There are a number of studies that document associations of epiphytes with cyanobacteria, but their functional importance remains similarly unclear. Cyanobacteria-containing coralloid roots are described for *Zamia pseudoparasitica* (Benzing 1990), *Nostoc* and other cyanobacteria are regularly found in the velamen of epiphytic orchids (Tsavkelova et al. 2003), and N-fixing bacteria were observed in the phyllosphere of many *Tillandsias* (Brighigna et al. 1992) and in the tanks of other bromeliad species (Fiore et al. 2007; Carrias et al. 2014).

5.4.6 Special Nutritional Modes Related to Animals

Animals may assist epiphyte nutrition either "voluntarily" or "involuntarily." The first case is given when, e.g., epiphytes trade carbohydrates and/or living space for nutrients in myrmecophytic, mutualistic relationships and the latter when plants are carnivorous. Treseder et al. (1995) have quantified the benefit that *Dischidia major* (Rubiaceae) receives from housing ants of the genus *Philidris*, Dolichoderinae. These ants frequently raise young and deposit debris such as dead ants, scavenged insect parts, or feces in sac-like "ant leaves." Using stable isotope analysis, Treseder et al. (1995) estimated that almost 30 % of the nitrogen in tissue of *Dischidia major* was derived from that debris. A direct demonstration of the transfer of nitrogen from ants to the host plant under field conditions was achieved with ^{15}N labeling experiments of ants and, respectively, the myrmecophytic fern *Myrmecophila sinuosa* (Gay 1993) and the myrmecophytic orchid *Caularthron bilamellatum* (Gegenbauer et al. 2012). Both species offer cavities as living space (hollow rhizomes or pseudobulbs) and the orchid *Caularthron bilamellatum* also carbohydrates in extrafloral nectaries. There are a number of additional myrmecophytic species among epiphytes described in the literature (Fisher and Zimmerman 1988; Huxley 1980), but a rigorous cost-benefit analysis of the trade-offs in this interaction has not been tried with any of them.

Carnivorous epiphytic plants are mostly found in particularly wet, nutrient-poor habitats (Benzing 1987). There are c. 1000 carnivorous species in the angiosperms, distributed over 17 genera in 9 families (Barthlott et al. 1987). More than 5 % of these are epiphytic, with 4 species of *Lentibularia* and 14 of *Utricularia* (both Lentibulariaceae, Table 2.1), and c. 30 *Nepenthes* spp. (Nepenthaceae). Whether the epiphytic bromeliad *Catopsis berteroniana* qualifies as carnivorous is contested. It has been demonstrated that this species attracts and captures substantially more arthropods than other tank bromeliads (Frank and Omeara 1984). Moreover, there are some features promoting carnivory such as UV reflection by leaves, epicuticular waxes, or a central tank, but other requisites of true carnivory are missing, e.g., prey digestion seems to be carried out exclusively by bacteria. To distinguish such species from true carnivores, it has become customary to call them "protocarnivorous." It is largely unclear whether epiphytic carnivores have any distinguishing characteristics from terrestrial congenerics. Benzing (1990) claimed that there were no obvious differences between terrestrial and epiphytic members of *Pinguicula* (Fig. 5.12) or *Nepenthes*, but provided no data to support this contention. The only study with pertinent data focused on *Utricularia* comparing biomass allocation patterns in terrestrial, aquatic, and epiphytic species (Porembski et al. 2006). Unfortunately, the inclusion of only a single epiphytic species limits interpretation. Compared to six terrestrial species, epiphytic *Utricularia quelchii* allocated twice as much biomass to leaves and 100 times more to traps, but less than

Fig. 5.12 Carnivorous *Pinguicula moranensis* plant on the trunk of a large oak tree in a Mexican Pine-oak forest at c. 2500 m a.s.l. Insert—Detail of flowering individuals (Photograph: Valeria Guzman)

half to reproductive structures. Such large structural differences are likely to reflect similarly pronounced functional variation, but the highly interesting system has not been studied in this regard.

5.4.7 Intraspecific Variation in Hemiepiphytes and Facultative Epiphytes

Many of the comparisons made above between epiphytic and terrestrial plants suffer from a potential phylogenetic bias. A possible way to avoid this bias is by studying different ontogenetic stages of hemiepiphytes or epiphytic and ground-rooted individuals of facultative epiphytes. In the former case, juvenile stages completely depend upon canopy resources, while later stages with contact to the ground can tap soil resources. The comparative study of plant water relations of epiphytic and ground-rooted conspecifics usually demonstrates that—unsurprisingly—soil contact leads to improved water supply (Zotz and Winter 1994a, b; Holbrook and Putz 1996; Liu et al. 2014). Nutrient supply, on the other hand, does not show a similarly consistent trend (Table 5.4). While all epiphytic *Clusia* spp.

Table 5.4 Nitrogen concentrations (% dry matter) in leaves of epiphytic and ground-rooted individuals of hemiepiphytes and facultative epiphytes

Species	Epiphytic	Terrestrial	Difference	Source
Clusia osaensis	0.8 ± 0.1 (4–40)	1.0 ± 0.1 (4–40)	↓	Wanek et al. (2002)
Clusia peninsulae	0.7 ± 0.1 (4–40)	1.0 ± 0.1 (4–40)	↓	Wanek et al. (2002)
Clusia rosea	1.29 ± 0.12 (18)	1.69 ± 0.16 (12)	↓	Ball et al. (1991)
Clusia uvitana	0.6 ± 0.1 (13)	0.9 ± 0.1 (25)	↓	Zotz and Winter (1994a, b)
Clusia valerii	0.6 ± 0.1 (4–40)	1.1 ± 0.1 (4–40)	↓	Wanek et al. (2002)
Schefflera rodriguesiana	1.68 ± 0.3 (20)	1.73 ± 0.2 (19)	n.s.	Feild and Dawson (1998)
Ficus benjamina	1.6 ± 0.4 (13)	1.33 ± 0.16 (10)	n.s.	Schmidt and Tracey (2006)
Ficus pertusa	2.7 ± 0.24 (5)	2.12 ± 0.28 (5)	↑	Putz and Holbrook (1989)
Ficus trigona	2.81 ± 0.24 (5)	1.59 ± 0.26 (5)	↑	Putz and Holbrook (1989)
Aechmea lingulata	0.84 ± 0.15 (12)	0.87 ± 0.15 (24)	n.s.	Ball et al. (1991)
Tillandsia utriculata	0.65 ± 0.01 (6)	0.65 ± 0.02 (6)	n.s.	Ball et al. (1991)
Anthurium acaule	1.87 ± 0.07 (6)	2.44 ± 0.1 (6)	↓	Ball et al. (1991)
Anthurium cordatum	2.33 ± 0.15 (6)	2.78 ± 0.14 (6)	↓	Ball et al. (1991)

Intraspecific differences were assessed with *t*-tests. Data are means ± SD (n). *Arrows* indicate significantly ($p < 0.05$) lower (↓) or higher (↑) concentrations in epiphytes (*t*-tests, $p < 0.05$); n.s. not significant had significantly lower leaf N, nitrogen levels in leaves of epiphytic *Ficus* and *Schefflera* tended to be higher or were statistically indistinguishable from those of soil-rooted conspecifics. No significant difference was found in facultatively epiphytic *Aechmea lingulata* and *Tillandsia utriculata* (Ball et al. 1991). The finding that both tank bromeliads have very low N concentrations irrespective of growing site may result from generally low nutrient requirements or alternatively from limited water and nutrient uptake by roots when growing on soil. In summary, studies with hemiepiphytes and facultative epiphytes do not suggest that epiphytes are generally more nutrient limited than ground-rooted species. Both plant groups could make excellent systems for a better understanding of nutrient relationships in tree canopies and should be used more often in future studies.

5.5 Photosynthesis, Carbon Gain, and Growth

Vascular epiphytes are autotrophs and engage in photosynthesis; there has been no evolution toward a holoparasitic habit. In the plant kingdom, there are three major types of photosynthesis, C_3-photosynthesis, C_4-photosynthesis (typically characterized by a *spatial* separation of CO_2 fixation via two different enzyme systems, anatomically distinguishable by leaves with “Kranz anatomy”), and Crassulacean acid metabolism (CAM), i.e., the *temporal* separation of nocturnal uptake of external CO_2 and actual fixation during daytime. Only two of these possibilities, C_3 and CAM, are found among epiphytes. (Whether unidentified poikilohydric *Tripogon* species, which sometimes occur epiphytically (Porembski 2011), use the C4-pathway has not been determined.) Why are there no C_4 epiphytes? One reason could be phylogenetic heritage—the major lineages with C_4 taxa (Poales and Caryophyllales) have hardly any epiphytic members (Table 2.1). Second, C_4 evolution is intimately associated with arid to semiarid regions (Sage et al. 2011), which are spatially separated from the hotspots of epiphytism. Finally, as pointed out by Sage (2004), C_4 compensates for high rates of photorespiration rather than helps against drought as such—consequently, even in dry forests and savannas, which are dominated by C_4 grasses, there is no evidence of epiphytes using C_4 photosynthesis (Mooney et al. 1989).

Crassulacean acid metabolism is prevalent among epiphytes not only in dry vegetation; a substantial proportion of CAM species can be found even in wet forests (Pierce et al. 2002b; Zotz 2004a). Orchids alone account for almost half of all CAM species globally with c. 8000 taxa (Silvera et al. 2010). The only known terrestrial orchids with CAM are in the Eulophiinae, an ancestrally epiphytic orchid lineage (Bone et al. 2015). All other plant families together just add a comparable number of species to the total (Smith and Winter 1996). Since a considerable proportion of the latter are also epiphytic (e.g., in the Bromeliaceae), epiphytic CAM species probably outnumber soil-rooted ones. (For a comparison of the biomass of epiphytic and terrestrial CAM plants, see Box 5.3.) It is interesting to note that the evolution of CAM and epiphytism are not necessarily tightly linked. A phylogenetic study with Bromeliaceae found quite independent trends in individual clades in respect to the occurrence of CAM and epiphytism (Crayn et al. 2004). However, while CAM is obviously not a *prerequisite* for the epiphytic lifestyle as such, its occurrence seems essential for the spread into drier habitats—the more xerophytic forms in this family are invariably CAM (Crayn et al. 2015).

Many physiological studies on epiphytes and hemiepiphytes specifically focused on CAM, but there is also a considerable body of literature on leaf gas exchange of C_3 epiphytes. Although most research was done in the greenhouse or in the laboratory, a number of field studies provide valuable insights into physiological responses to the complex variation in abiotic conditions in situ (Lüttge et al. 1986; Pierce et al. 2002a; Griffiths and Maxwell 1999; Griffiths et al. 1989; Zotz and Winter 1994a).

Box 5.3 CAM Biomass in Epiphytes and Terrestrial Plants

Although it becomes increasingly clear that tropical forest canopies are the global hotspot of CAM species in terms of diversity (Winter and Smith 1996), this probably does not translate in a similar importance in terms of CAM biomass at a local and global scale. Even in montane forests, where C_3 and CAM epiphytes can make up several tons per hectare (Table 9.1), they still contribute less than 1 % to the total forest biomass (Edwards and Grubb 1977; Tanner 1980). Since the proportion of CAM species decreases from the lowlands to montane forests (e.g., Hietz et al. 1999; Griffiths et al. 1986), the absolute biomass of CAM epiphytes may increase rather little with altitude, but may actually decrease and drop to zero in upper montane forests (Earnshaw et al. 1987). For example, in a montane forest in Mexico at an altitude of 1980 m a.s.l., CAM species make up 8 % of the epiphyte flora, but less than 2 % of their biomass, accounting for c. 6 kg ha^{-1} (Hietz and Hietz-Seifert 1995 and Hietz, unpubl.). In the lowlands, CAM biomass was even lower: Zotz (2004a) gives an estimate of c. 3 kg ha^{-1} for the San Lorenzo area in Panama.

Biomass estimates of CAM plants from arid areas may exceed these figures by several orders of magnitude. For example, in the arid loma vegetation in northern Peru, the terrestrial CAM species, *Tillandsia latifolia*, alone reaches more than 1600 kg ha^{-1} (Rundel and Dillon 1998). Large cacti in North American deserts or the succulent Karoo may reach similar values (MacMahon and Wagner 1985; Milton 1990). This suggests that most CAM biomass—at a global scale—is found in semi-deserts and other semiarid biomes. This conclusion seems robust, even when taking into account the larger land area covered by tropical and subtropical forests compared to semi-deserts (approx. a factor of 3, Olson et al. 1983). In addition, terrestrial CAM plants from arid biomes may not only account for more standing biomass than epiphytic CAM plants, but also show much higher potential productivity:

(continued)

Box 5.3 (continued)
while growth in vascular epiphytes seems to be inherently slow (Chap. 5), some terrestrial *Agave* and *Opuntia* species reach annual productivities under favorable conditions that are among the highest for any plant (Nobel 1996).

5.5.1 Foliar Carbon Gain

Maximum rates of net CO_2 uptake under saturating light and otherwise near-optimal conditions (A_{max}) have been reported for more than 80 species of vascular epiphytes (Fig. 5.13). The average A_{max} of 3.0 ± 1.9 μmol CO_2 m^{-2} s^{-1} (±SD) is just about 20 % of what is typically found in herbaceous plants in exposed situations and even lower than typical values for soil-rooted shade plants (Larcher 2003). Overall, the low values of A_{max} come as no surprise, but conclusions should still be drawn with caution, because the dataset is strongly unbalanced taxonomically (e.g., >20 % of all data points stem from just two studies with representatives of two genera, *Cattleya* and *Hymenophyllum*, Andrade-Souza et al. 2009; Parra et al. 2009), and there are large differences in the methodology and used plant material (e.g., field and greenhouse studies). Moreover, there is uneven participation of species from exposed and shaded sites. To date, the highest documented A_{max} is *c*. 8 μmol CO_2 m^{-2} s^{-1} (Andrade-Souza et al. 2009; Zotz and Winter 1994a); low values of <1 μmol CO_2 m^{-2} s^{-1} are found, e.g., in some filmy ferns (Hietz and Briones 2004). The average A_{max} clearly suggests that epiphytes as a group are not tuned toward high productivity.

There are some straightforward explanations for the observed variation in A_{max}. For one, differences should be related to the vertical light gradient within a forest. Stuntz and Zotz (2001) quantified its effect on photosynthetic parameters in

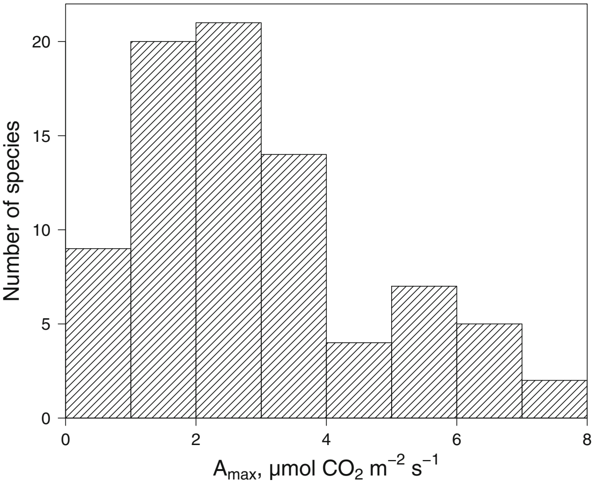


Fig. 5.13 Histogram of A_{max}, the maximum rates of net CO_2 uptake of foliar organs (or cladodes in the case of two cacti), under saturating PFD and otherwise near-optimal conditions for >80 species of vascular epiphytes (from diverse sources)

27 epiphyte species on Barro Colorado Island, Panama. The average rate of area-based photosynthesis increased threefold from species typically growing in the understory to those found in the upper canopy, with intermediate values for mid-story species. All other characteristic of light response curves, e.g., light compensation points, also varied as expected for plants in general along a PFD gradient (Larcher 2003). Such differences are suggestive of a relatively simple physiological mechanism behind the vertical segregation observed in many epiphyte communities (Chap. 7), although this conclusion rests on the assumption of a limited potential of each species to acclimate to different abiotic conditions. This aspect is little studied, but at least some species seem to be quite plastic in their physiological responses (Martin et al. 1999). Taxonomy also seems to leave an imprint on photosynthetic capacity. For example, bromeliads tend to have lower A_{max} than, e.g., orchids, while ferns as a group are not significantly different from angiosperms. This is somewhat surprising, since ferns as a group typically show relatively low A_{max} (Larcher 2003). Considering that the data stem from many studies and do not control for variation in microhabitat, this conclusion has to be taken cum grano salis. Differences in A_{max} could also be related to photosynthetic pathway, as CAM plants usually show lower capacity for CO_2 uptake than C_3 species (Larcher 2003). However, this expectation is not met in the current dataset: there is no difference in A_{max} between these two groups (29 CAM species: 3.1 ± 2.0 μmol m^{-2} s^{-1}; 52 C_3 species: 3.0 ± 1.8 μmol m^{-2} s^{-1}; means ± SD).

In the field, plants will rarely reach the documented maxima of net CO_2 uptake under near-optimal conditions, mostly due to insufficient water supply and non-saturating PFD (Fig. 5.2, Zotz and Winter 1994a). However, since values of A_{max} have been shown to be good predictors of daily integrated carbon gain (Zotz and Winter 1993), repeated determinations of A_{max} should allow reasonable estimates of long-term carbon gain. A comparison of two C_3 epiphytes and a CAM epiphyte from a seasonal lowland forest revealed a surprisingly similar annual foliar carbon budget of c. 1000 g CO_2 m^{-2} a^{-1} (Zotz and Winter 1994a).

5.5.2 Carbon Gain by Non-foliar Organs

Non-foliar organs of epiphytes (stems, fruits, roots) are frequently green and should improve plant carbon budgets. Particularly the exposure of roots to light offers unique opportunities to reduce the carbon costs of these usually heterotrophic organs—photosynthesis in roots is largely distinctive for epiphytes (but compare aerial roots in mangroves, Gill and Tomlinson 1977). In the extreme case, in so-called leafless epiphytic orchids like *Chiloschista usneoides*, roots are the only photosynthetically active organs (Benzing et al. 1983; Cockburn et al. 1985). Excluding the possibility of mycotrophy, these plants must obviously be able to achieve a positive carbon balance via photosynthesis (Cockburn et al. 1985), whereas it remains disputed whether aerial roots of species with green leaves are capable of *net* CO_2 uptake from the atmosphere. While Benzing and Ott (1981) found constant release of CO_2 from such roots during day and night in eight of nine tested species, Dueker and Arditti (1968) reported net CO_2 uptake in roots of three other species that even exceeded the uptake rates of their leaves. The evidence for the photosynthetic pathway used by roots is less controversial: most orchid roots fix carbon via the C_3 pathway even in species with leaves engaging in CAM (Martin et al. 2010; Moreira et al. 2009), whereas roots of all tested leafless orchids engage in CAM (Benzing and Ott 1981; Cockburn et al. 1985).

Stem photosynthesis has only been studied in some detail in leafless cacti. Similar to soil-rooted Cactaceae, the flattened stems (platyclades) take over the function of leaves with maximum rates in the range of leaves in other epiphytes (Andrade and Nobel 1996). The contribution of green stems to the whole plant carbon budget in other taxa is largely unexplored.

Reproductive allocation (defined as the proportion of biomass or nutrients invested in reproductive structures) is generally high in vascular epiphytes (up to 26 % of total plant biomass, Table 5.3). In contrast to water and nutrients, which always have to be supplied to developing fruits by the remaining plant, the carbon costs of reproduction can be reduced by the fruit via photosynthesis (Lambers et al. 2008). Available evidence suggests that this is achieved by recycling of respiratory CO_2 rather than by net uptake (Zotz et al. 2003; Benzing and Pockman 1989). Besides lowering the carbon cost of reproduction, Benzing and Pockman (1989) noted an additional advantage: CO_2 fixation in fruit occurs with hardly any water loss. Based on diel patterns of gas exchange and nocturnal acidification, Zotz et al. (2003) quantified the contribution of CO_2 recycling for two epiphytic orchids. Mature *Dimerandra emarginata* fruits reduced CO_2 losses by more than 60 %, while the reduction in mature *Caularthron bilamellatum* fruits was much smaller and amounted to only c. 10 %.

5.5.3 Whole Plant Carbon Budgets

Y-Plant, a three-dimensional shoot architecture model developed by Pearcy and Yang (1996), is a very useful tool to scale up carbon exchange from individual leaves to the entire foliage of a plant. In spite of its usefulness and relative ease of application, there is only a single study with epiphytes using Y-plant: Zotz et al. (2002) used this program to study the relative importance of size-related changes in physiology and morphology in a tank bromeliad, but Y-Plant can also be used to explore the functional consequences of different tank morphologies (Fig. 5.14). In these bromeliads, which feature a very high leaf mass ratio, the modeled carbon budgets are probably close to whole plant carbon budgets and—in the absence of reproduction—also provide insights into expected growth rates. In all other cases, however, the relationship of A_{max} and growth is far from straightforward, similar to the situation in plants in general (Lambers et al. 2008). There are few attempts to investigate the carbon metabolism of the different major organ types, i.e., leaves, shoot, and roots, in an integrated manner for any vascular epiphyte. An exception is Rodrigues et al.'s (2013) study on the temporal changes of gas exchange and CAM activity in a thick and a thin-leaved orchid during

Fig. 5.14 Y-Plant, a three-dimensional shoot architecture model developed by Pearcy and Yang (1996), allows the reconstruction of real plants and the upscaling of CO_2 uptake data from single leaves to the entire plant. By manipulating physiological and morphological features, it allows the user to assess the effect of particular traits on whole plant carbon gain. Although originally designed for simple plain leaves, it is possible to model curved forms as well. Shown are modeled individuals of *Vriesea ringens, Tillandsia monadelpha, and Guzmania minor* (drawings by Joachim Beyschlag)

drought. *Cattleya walkeriana*, a CAM orchid, upregulated CAM in its thick leaves but not in its pseudobulbs and roots. In contrast, thin-leaved *Oncidium* "Aloha" reduced leaf gas exchange almost completely, but switched from C3 photosynthesis to facultative CAM in its non-foliar organs. Aerenchyma ducts connect pseudobulbs and leaves, which may facilitate the recycling of respiratory CO_2 from leaf tissues in adjacent pseudobulbs. Although this study does not allow a quantitative evaluation of the contribution of different compartments to whole-plant carbon budget, it demonstrates fascinating physiological diversity and calls for a more integrative approach in the study of carbon economy beyond leaf gas exchange.

5.5.4 Light Flecks and Carbon Gain

Low levels of diffuse light, punctuated from time to time by bright lightflecks, are typical for understory habitats (Chazdon and Fetcher 1984). The capacity of plants to exploit these brief periods of high photon flux density (PFD) for carbon gain is crucial in such light-limited habitats and has been studied extensively in soil-rooted plants (e.g., Pearcy 1990; Allen and Pearcy 2000). Typically, understory plants show relatively high stomatal conductance (g_w) during periods of low light and fast induction, which improves the capacity to utilize lightflecks for carbon gain, but inevitably leads to increased water loss (Pearcy 1990). Zotz and Mikona (2003) hypothesized that epiphytic plants should behave differently from soil-rooted herbs and shrubs because of the overriding importance of water scarcity in the epiphytic habitat. The results of a field and laboratory study with the understory orchid *Aspasia principissa* only partly agreed with specific expectations: induction during

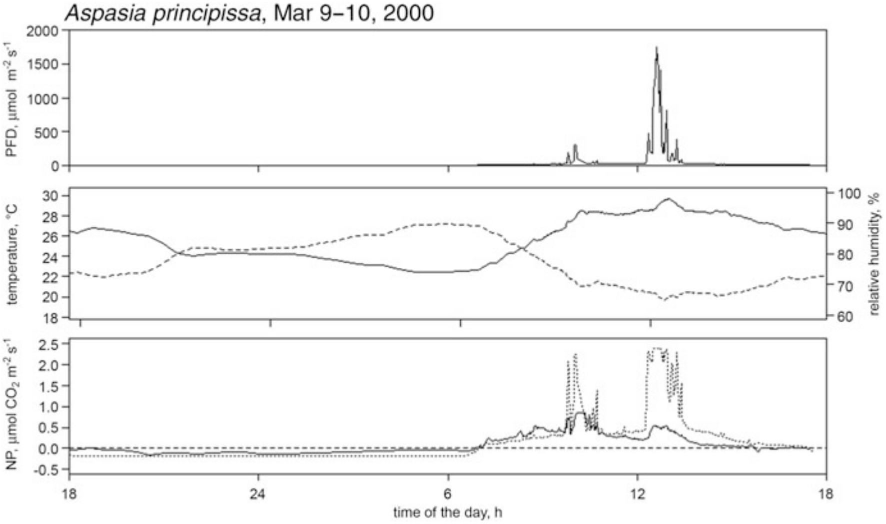


Fig. 5.15 Diel course of environmental parameters and leaf gas exchange of *Aspasia principissa* in the understory of a moist lowland forest on Barro Colorado Island, Panama. Shown are PFD (photon flux density at the leaf level), air temperature (*solid line*), and relative humidity (*dashed line*) near the leaf and measured CO_2 gas exchange. The *dotted line* in the lowermost plot represents modeled rates based on steady-state gas exchange rates of fully induced leaves. The *dashed line* indicates zero gas exchange. Modified after Zotz and Mikona (2003)

light flecks was indeed very slow, but induction loss was not particularly fast. The two observations may be related: if an epiphyte rarely reaches maximum stomatal aperture in the field, the negative impact of slow induction loss on the water balance is negligible and selection may not have acted against it. Irrespective of the underlying physiological reasons, these observations seem to be representative for other epiphytes as well. A comparative study with several epiphytic and terrestrial ferns yielded consistent results (Zhang et al. 2009). The consequences of slow induction for carbon gain can be quantified by comparing the measured CO_2 uptake with that expected in the absence of induction. On the particular day shown in Fig. 5.15, the possible carbon gain would have been twice as high, and the average of the five diel measurements still indicated an about 50 % higher potential carbon gain (Zotz and Mikona 2003).

5.5.5 Photoinhibition

The light conditions that epiphytes experience in the field span the entire range from deep shade in the understory to excessive light in the outer canopy. Incident radiation may vary (a) in the short term during lightflecks as described in

Sect. 5.5.4, (b) relatively predictably over the course of a day, (c) unpredictably for longer periods after changes in canopy structure (e.g., when shading branches break or neighboring trees fall), or again (d) predictably with the season, with particularly pronounced differences in drought-deciduous trees (Einzmann et al. 2015). Excessively high levels of irradiance can lead to short- and long-term reductions in carbon gain via photoinhibition, in the extreme case making growth at exposed sites impossible for a given species.

The physiological response of epiphytes to different light regimes has received a fair amount of attention: almost 40 studies have been published during the last three decades that have addressed photoinhibition in epiphytes, both in the field (e.g., Zotz and Tyree 1996; Tausz et al. 2001) and in the laboratory (e.g., Maxwell et al. 1994; Ruban et al. 1993). These studies, which often included a combination of both high light and drought stress, usually did not quantify the *reduction* in carbon gain but rather quantified aspects of photoinhibition/photoprotection via fluorescence analysis or the analysis of pigments such as xanthophylls. The former provides information on the functioning of photosystem II, while the xanthophyll cycle represents an important mechanism of photoprotection via the thermal dissipation of excess energy.

The light energy absorbed by chlorophyll molecules can be used in three ways—it can drive photosynthesis, it can be dissipated as heat, or it can be reemitted as light, i.e., as chlorophyll fluorescence (Maxwell and Johnson 2000). Given the generally low level of net photosynthesis in epiphytes (Fig. 5.13), it had been assumed that sun epiphytes must have a large capacity for radiationless dissipation of energy. First unambiguous evidence for this notion was provided under laboratory conditions by Ruban et al. (1993) for *Guzmania monostachia*. In another study with the same species, Maxwell et al. (1994) were able to show that the capacity for downregulation of photosynthesis under high light and drought stress was associated with a large pool of xanthophylls with a high proportion of zeaxanthin, an effective antioxidant. Under well-watered conditions in the field, epiphytic orchids like *Dimerandra emarginata*, which typically occur under fully exposed conditions, show only transient diurnal reductions in potential quantum yield (Zotz and Tyree 1996), again arguing for a high capacity for photoprotection. Probably the most complete field study on this topic was done by Manzano et al. (2015). These authors studied five epiphytic orchid species in two tropical dry forests over an entire year, quantifying fluorescence parameters, xanthophyll concentrations, and titratable acidity in these CAM plants. Their results were consistent with the findings described above, but added the observation that—during stressful conditions—zeaxanthin was retained at night. Nocturnal retention of this antioxidant had been reported previously for ground-rooted plants under low temperature or drought stress (e.g., Barker et al. 2002). Manzano et al. (2015) concluded that in spite of a high capacity to cope with the environmental challenge of severe drought and high radiation during the dry season in Yucatán peninsula, the studied orchids cannot completely avoid photoinhibition.

5.5.6 Growth

Growth, reproduction, and survival represent three competing demands for a finite supply of resources (Grime 1977). Allocation of resources to growth is thus almost inevitably associated with a trade-off, e.g., reduced reproduction. Grime's (1977) three primary strategies conceptualize the different options and allow predictions: plants from stressful and low-resource environments, such as epiphytes, are expected to show low relative growth rate (RGR). Similar predictions can be made using a quite different approach, i.e., trait dimensions (Westoby and Wright 2006). The five traits leaf mass per area (LMA), leaf N concentration, leaf life span, potential photosynthesis, and dark respiration explain almost 80 % of worldwide variation in plants. Epiphytes are clearly at the "slow-return" extreme of the leaf economics spectrum (Wright et al. 2004) with low nutrient concentrations (Fig. 5.10), long leaf live span (Zotz 1998), high LMA, and low rates of photosynthesis (Fig. 5.13).

The available database confirms expectations of slow growth rates (Table 5.5). Although one has to acknowledge a substantial taxonomic bias (about 50 % of all data are from *Tillandsia* spp.), there is currently only one possible conclusion: vascular epiphytes are inherently *very* slow-growing. Actually, RGRs which average 6 ± 4 mg g^{-1} day^{-1} are lower than those of slow-growing conifers by almost one order of magnitude (Grime and Hunt 1975). Noteworthy, this is growth under near-optimal conditions in the greenhouse or growth chamber. In situ RGR reaches substantially lower values, e.g., averaging 1.3 mg g^{-1} day^{-1} in the case of *Vriesea sanguinolenta* in lowland Panama compared to 11.2 mg g^{-1} day^{-1} in the greenhouse (Schmidt and Zotz 2002). There are claims of "fast growth" in terrestrial *Epidendrum* species like *E. radicans* (Pridgeon et al. 2005), but such assertions have not been backed up with actual data, or compared with RGR of epiphytic members of that genus.

Variation in RGR can be either related to physiology, i.e., differences in net photosynthesis, or differences in allocation patterns at the plant level, i.e., varying investment in leaf area (Lambers et al. 2008). This relationship is expressed in the following formula:

$$\mathrm{RGR} = \mathrm{LAR} \times \mathrm{NAR},$$

in which NAR is net assimilation rate (the increase in plant mass per unit leaf area) and LAR is leaf area ratio (the amount of leaf area per unit plant mass). The latter can in turn be expressed as the product of specific leaf area (SLA, the amount of leaf area per unit leaf mass) and leaf mass ratio (LMR, the fraction of the total plant biomass allocated to leaves).

There is considerable debate on the nature of variation in RGR—while some assert that SLA is usually the major driver (Lambers et al. 2008), others identify NAR as generally more important (Shipley 2006). There is a single published study which performed a classical growth analysis with epiphytes: Zotz and Asshoff (2010) studied growth in juveniles of three epiphytic bromeliads as a function of

Table 5.5 Relative growth rates (RGR in mg g^{-1} day^{-1}) in vascular epiphytes

Species	Family	RGR	Source/Comments
Vriesea sanguinolenta	Bromeliaceae	11.2	Schmidt and Zotz (2002), Zotz and Asshoff (2010)
Guzmania monostachia	Bromeliaceae	8.5	Zotz and Asshoff (2010)
Tillandsia elongata	Bromeliaceae	11.1	Zotz et al. (2010)
Tillandsia flexuosa	Bromeliaceae	17	Zotz (2009)
Tillandsia guatemalensis	Bromeliaceae	7	Castro-Hernández et al. (1999)
Oncidium "Goldiana"	Orchidaceae	4.5	Li et al. (2002b)
"Mokara Yellow"	Orchidaceae	6.8	Li et al. (2002a)
Oncidium praetextum	Orchidaceae	1.7	Monteiro et al. (2009)
Bulbophyllum longissimum	Orchidaceae	1.9	Monteiro et al. (2009)
Aechmea fasciata	Bromeliaceae	3.8	Monteiro et al. (2009) at 560 ppm CO_2
Vriesea "Splenriet"	Bromeliaceae	5.4	Monteiro et al. (2009) at 560 ppm CO_2
Catopsis juncifolia	Bromeliaceae	5.5	Monteiro et al. (2009) at 560 ppm CO_2
Tillandsia juncea	Bromeliaceae	4.3	Zotz et al. (2010)
Tillandsia viridiflora	Bromeliaceae	3	Zotz et al. (2010)
Tillandsia subulifera	Bromeliaceae	4.4	Zotz et al. (2010)
Tillandsia fasciculata	Bromeliaceae	7.4	Zotz et al. (2010), Monteiro et al. (2009)
Catopsis sessiliflora	Bromeliaceae	5.5	Zotz and Laube (2005)
Synopsis			
Epiphytes (average)		6 ± 4	
Conifers (average)		41 ± 10	Grime and Hunt (1975)
Herbs (average)		114 ± 24	Grime and Hunt (1975)

Only studies, in which growth was determined on a dry mass basis under controlled, presumably optimal conditions, are considered. In a few cases, when a species was studied more than once, only the higher RGR value is shown. Data are means (±SD)

different nutrient supply, demonstrating a strong correlation between RGR and NAR and none with the other components SLA, LMR, or LAR. However, their conclusion that changes in RGR are almost exclusively a function of NAR could have been premature, because their experiment lasted for only 11 weeks, during which only few new leaves were produced. It takes about a year for these tank bromeliads to replace old foliage completely by new one (Schmidt and Zotz 2000). Thus, this analysis demonstrated a short-term physiological response, but could have missed a possibly different long-term response. Box 5.4 describes a study that provides unambiguous evidence that this is not the case: differences in RGR in the bromeliad *Vriesea sanguinolenta* observed after 1 year of experimental treatments were almost exclusively related to difference in NAR.

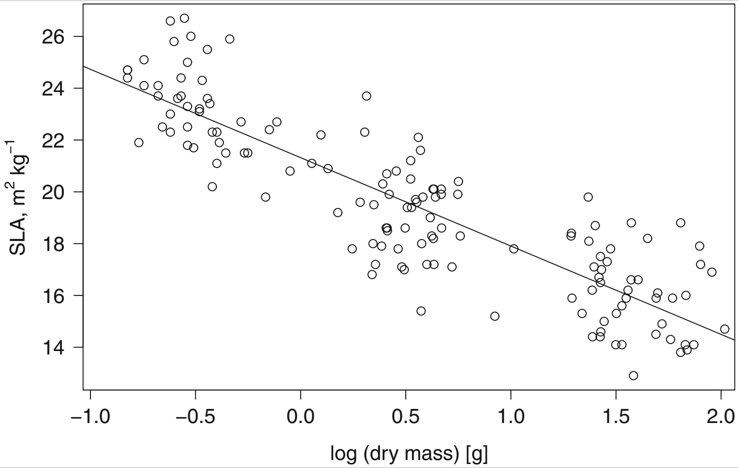
Box 5.4 Growth Analysis in *Vriesea sanguinolenta* (Stefan Wester, Cord Mikona, and Gerhard Zotz)

Vriesea sanguinolenta is a conspicuous tank bromeliad found in moist forests from Costa Rica to Colombia. As described in detail in Laube and Zotz (2003), an experiment was set up in a large forest gap near the laboratory facility on Barro Colorado Island, Panama: 140 plants were exposed to two levels of light (L+/L−), nutrients (N+/N−), and water supply (W+/W−) in a full-factorial design from May 2001 through April 2002. Plants covered a size range of 4–39 cm (LL, length of longest leaf) and were grouped into three size classes (small: 4–6, medium: 13–17, large: 30–39 cm LL).

At the end of the experiment, the following measurements were taken: photosynthetic capacity in an oxygen electrode under saturating CO_2 and light levels, total leaf area, total leaf dry weight, stem dry weight, leaf thickness, and leaf N concentration. These values allowed the calculation of relative growth rate (RGR), specific leaf area (SLA), LMR (leaf mass ratio), leaf area ratio (LAR), and net assimilation rate (NAR).

Allometric changes

Irrespective of treatment conditions, several plant parameters changed regularly with size, e.g., SLA decreased log-linearly from the smallest to the largest individual (Pearson Product moment correlation, $r^2 = 0.77$, $p < 0.05$, range 13–27 $m^{-2}\ kg^{-1}$), which corresponds to a linear increase in leaf thickness by some 50 % from 0.3 to 0.45 mm. While leaves invariably made up the dominant proportion of plant dry mass in these bromeliads, the relative proportion of the stem increased about threefold over the range of studied individuals: LMR decreased log-linearly from >0.95 in the smallest plants to <0.85 in the largest plants (Pearson Product moment correlation, $r^2 = 0.56$, $p < 0.05$).



(continued)

Box 5.4 (continued)

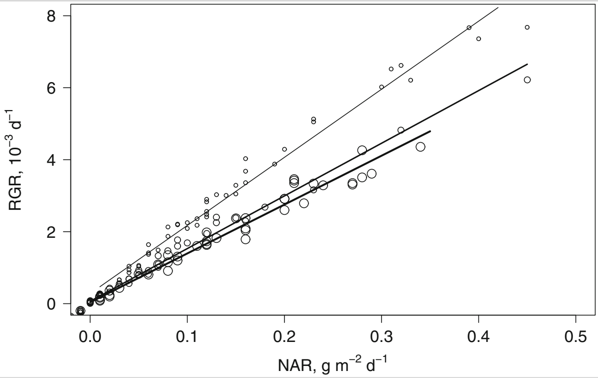
Photosynthesis

The area-based photosynthetic capacity of the youngest, fully expanded leaf ranged from 2.2 to 13.4 μmol O_2 m^{-2} s^{-1}. It was significantly affected by nutrient supply, light, and initial size (3-way ANOVA, $p < 0.05$), while on a mass basis, only higher leaf nitrogen concentrations influenced photosynthetic capacity (3-way ANOVA, $p < 0.05$).

Relative Growth Rates

As in other epiphytes, growth in the studied plants was slow. Even under the best combinations of water, nutrient, and light, the highest RGR did not exceed 8 10^{-3} day^{-1}. All studied factors significantly influenced RGR, but rarely independently of each other. For example, RGR was increased at high light by more than 50 %, but only when nutrient supply was high. This difference was consistently found in all size classes. Both improved water and nutrient supply acted in a synergistic fashion, but their effects and interaction were size dependent. Consistent with the results of an experiment of shorter duration (Laube and Zotz 2003), the strongest stimulation of RGR was observed in small individuals with an increase from 1.1 10^{-3} day^{-1} under low light/low water conditions to 5.7 10^{-3} day^{-1} under high light/high water conditions. SLA was consistently affected by light with an average reduction of SLA in high light of 11 %.

The relative growth rate correlated closely with net assimilation rate (NAR), which in turn was closely related to area-related photosynthetic capacity. Specific leaf area, on the other hand, did not correlate with RGR nor did LMR. The relationship of NAR and RGR differed among size classes as shown in the following graph.



The slopes of the different size classes (symbol size and line thickness indicate small, medium, and large plants) differ significantly, ANCOVA, $p < 0.05$). In the smaller plants, a significantly steeper slope led to a higher

(continued)

Box 5.4 (continued)

RGR for a given NAR. This difference coincides with a significantly higher LMR in smaller plants.

Conclusions

It is debated whether variation in RGR is primarily related to variation in SLA (Lambers et al. 2008) or in NAR (Shipley 2006). The described results support earlier conclusions based on an experiment of rather short duration (Zotz and Asshoff 2010): NAR is the major factor associated with variation in RGR in the studied tank bromeliads. The duration of our experiment (almost 1 year) was long enough to allow the production of an entire new set of leaves. The fact that SLA varied significantly with light environment in all size classes clearly indicates that the time frame was sufficient for possible changes in morphological parameters to develop in these very slow-growing plants.

5.5.7 Atmospheric CO_2, Net CO_2 Uptake, and Growth

The concentration of CO_2 in the atmosphere has continuously increased since the onset of the industrial revolution and is expected to rise even more in future decades (Solomon et al. 2007). The rate of photosynthetic CO_2 uptake is not saturated in C3 plants under current conditions (Körner 2003); hence epiphytes could actually profit from this development because of improved water use efficiency. A few studies have focused on the effects of elevated CO_2 on epiphytes (e.g., Monteiro et al. 2009; Raveh et al. 1995; Li et al. 2002a), but the interaction with other important factors (e.g., water and nutrient supply) has rarely been analyzed. Studying CO_2 in isolation may be problematic for an ecologically meaningful interpretation for the following reasons: (1) Water supply is assumed to be the most important environmental factor for most epiphytes (Zotz and Hietz 2001) and (2) both water and nutrient availability generally influence the effect of CO_2 (Saxe et al. 1998). Indeed, when both CO_2 and water supply were manipulated in 11 epiphytic bromeliad species in a growth chamber study (Zotz et al. 2010), growth was only stimulated by CO_2 in a single species, while the majority of species showed the expected effect of different water supply. With the exception of two species, the expected mitigation of drought stress by elevated CO_2 was not found.

To summarize, current evidence does not support the notion that elevated CO_2 will substantially increase growth and water use efficiency among vascular epiphytes. However, this conclusion is based on a very limited number of studies. Considering that epiphytes have been called “especially vulnerable” to global change (Benzing 1998), a much greater research effort seems warranted to allow better predictions of the potential consequences of increased CO_2 and other aspects of global change for epiphytes. Last but not least, such experiments should also address possible interactions of the abovementioned factors with increasing temperatures.

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Population Biology

6

6.1 Diaspores

Schimper (1888) was the first to point out that seed characteristics probably acted as a major filter in the evolution of epiphytism. However, in spite of the dominance of taxa with tiny, anemochorous diaspores among epiphytes (e.g., orchids and ferns, Chaps. 2 and 4), small seeds are neither a *necessary* nor a *sufficient* prerequisite for epiphytic existence. As mentioned earlier, direct comparisons of epiphytic and non-epiphytic members of Rubiaceae, Gesneriaceae, and Melastomataceae (Rockwood 1985) show that seed weights of epiphytes can be comparable to, or even exceed, those of terrestrial species.

There is first solid evidence that diaspores of epiphytes are effective dispersers within tree crowns. A comparison of seeds in seed traps in the canopy (c. 20 m above the forest floor) with those on the ground near a common tree species in Monteverde (Sheldon and Nadkarni 2013) yielded an average number of 13 epiphyte species in the former and only 8 species in the latter. Diaspores of ground-rooted life forms (small and large trees, lianas), on the other hand, were collected in both strata about equally. Unfortunately, the epiphytes included in this study were mostly bird dispersed, which is rather atypical for epiphytes (Sect. 4.7): the used methodology did not allow sampling of, e.g., orchid seeds. Thus, we are still lacking field studies of a representative sample of a local epiphyte community, let alone a more sophisticated analysis of the aerodynamic properties of epiphyte diaspores.

Is there a seed bank in epiphytic soils? Generally, fast germination and limited seed longevity argue against the existence of a seed bank of epiphytic taxa (e.g., Winkler et al. 2005; Cota-Sanchez and Abreu 2007). However, a number of studies provide convincing evidence for a seed bank in canopy soils and in organic material in leaf sheaths of palms (Nadkarni and Haber 2009; Nadkarni and Solano 2002; Correa et al. 2012), but the detected species are mostly terrestrial, gap-colonizing tree species, accompanied by a few fruticose or suffruticose hemiepiphytes in genera like *Neomirandea*, *Lycianthes*, or *Blakea*. Thus, in contrast to the common

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situation in terrestrial habitats (Crawley 1997), seed banks are unlikely to play a major role in epiphyte population and community dynamics.

6.2 Germination and Establishment

Germination and subsequent establishment are key dimensions of the regeneration niche (Grubb 1977). The proportion of successfully germinating seeds is usually quite low under natural conditions (Benzing 1978; Toledo-Aceves et al. 2012; Winkler et al. 2005; Mondragón et al. 2004b). This is usually not due to the production of many nonviable seeds, because laboratory trials tend to yield near-complete germination success in most cases (Benzing 1978; Toledo-Aceves et al. 2012; Correa and Zotz 2014; see also Box 6.1). None of the studies on germination has been able to elucidate the reasons for this discrepancy, e.g., desiccation, physical dislodging, pathogen attack, or predation by ants as observed during a germination experiment with bromeliad seeds (G. Zotz, unpubl. obs.). The observation of increased germination success in terrestrial orchids close to conspecific adults (probably because of contact with mycorrhizal fungi, compare Diez 2007) may be relevant for epiphytes as well. However, the only study investigating this aspect in the field in the case of the epiphytic orchid, *Epidendrum firmum* (Kartzinel et al. 2013), found no support for this notion. Contrasting evidence from a single species is obviously not enough to discard the possibility of such positive neighborhood effects. The role of mycorrhizal fungi in epiphytes remains generally little understood (Chap. 8), but there have been first promising attempts in the development of field methods to study fungal infections during germination in situ (Zettler et al. 2011), which should allow informative studies in the future.

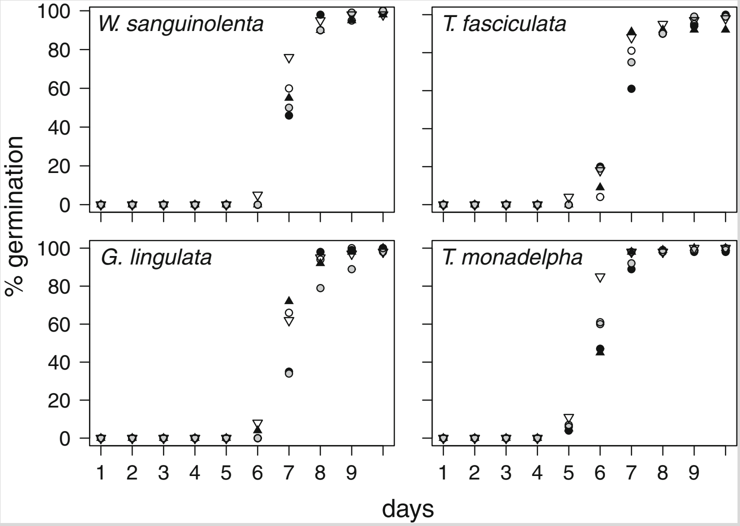
Box 6.1 Light Quality and Germination in Epiphytic Bromeliads (Eva-Maria Voß mann, Stefan Wester, and Gerhard Zotz)

Differences in seed germination response to light quality may promote coexistence in terrestrial habitats (Daws et al. 2002). We tested the hypothesis put forward by Benzing (1978) that light quality could also affect germination in epiphytic plants that normally grow at exposed sites (*Vriesea sanguinolenta*, *Tillandsia fasciculata*) and two understory species (*Tillandsia monadelpha*, *Guzmania minor*). Mature seeds were pretreated as described elsewhere (Bader et al. 2009) and kept constantly moist in closed Petri dishes (4 replicates of 15 seeds per species) in climate chambers (Economic Delux, Snijders Scientific, Tilburg, The Netherlands). Conditions were 25 °C, 12 h/12 h light/dark periods. Following Daws et al. (2002), coated polyester filters (Lee Filters, London, UK) were used to achieve red to far-red ratios (R:FR) of 0.08, 0.15, 0.21, 0.47, and 1.37, which represent a decreasing degree of openness. As shown in the following figure, germination was near complete (>90 %) in about 7 days, independent of species and treatment. (Data are

(continued)

Box 6.1 (continued)

means of four replicates. SD not shown for clarity. The average SD for the days 5–10 was 8 %, on the remaining days close to zero.)



These results suggests that light quality does not play a role in determining the vertical stratification in species occurrence. Moreover, a second run in complete darkness (6 replicates of 10 seeds per species) indicated that light was not even necessary to trigger germination in two species. About 50 % of the seeds of *Tillandsia fasciculata* and *Tillandsia monadelpha* germinated in the dark within 10 days. These seedlings were white, but the extruding hypocotyl usually turned green very fast once exposed to light. Interestingly, these results are at odds with data from the only other study on this topic we are aware of (Pereira et al. 2009). These authors found reduced germination in two facultatively epiphytic *Vriesea* species at R:FR ratios <0.2.

The importance of light for the germination process in epiphytic habitats is thus far from unambiguous. Vasudevan and Van Staden (2010) found that both germination percentage and growth of rhizoids on developing protocorms were enhanced by dark pretreatment of the seeds of the orchid, *Ansellia africana*, and Rasmussen et al. (2015) supposed that inhibition of germination by light could assure that seeds sink into organic substrate to escape desiccation after germination. This is, of course, pure speculation, but the idea is interesting enough to warrant a closer look at the way light affects germination in epiphytes.

Both light quality and quantity can influence germination, and conceivably light requirements could differ between epiphytes and terrestrial plants. Although many epiphytic bromeliads (Downs 1964) or ferns (Raghavan 1971) meet this expectation and do not germinate in darkness, there are quite a large number of epiphytic bromeliads, orchids, or ferns that do not require light for germination (e.g., Fernandez et al. 1989; Arditti 1967; Shull 1911, Box 6.1). The hypothesis that light *quality* may influence germination in epiphytes similar to terrestrial taxa (Benzing 1978), thus representing a possible physiological mechanism behind vertical stratification, is not supported by data either (Box 6.1).

The effects of other important environmental factors, e.g., water availability and temperature regime, on germination of vascular epiphytes are briefly discussed in Sect. 5.2. Water availability is not only a major factor for germination success, but also for early establishment. Not surprisingly, first-year survival is usually strongly correlated with rainfall in a particular year (Zotz and Schmidt 2006; Zotz et al. 2005; Olaya-Arenas et al. 2011).

Vivipary, i.e., the germination of seeds before being shed from the parent plant, is not very common in the plant kingdom with just about 100 known cases (Elmqvist and Cox 1996), and there is no indication that vivipary is particularly frequent among epiphytes. However, there are a few reports of vivipary among epiphytic cacti and bromeliads (e.g., Cota-Sanchez and Abreu 2007; Harshberger 1910). Whereas the observation in *Tillandsia tenuifolia* (Harshberger 1910) is enigmatic because there is no obvious advantage of germination in a dry pod, a fleshy cactus fruit may provide a moist environment for germination under otherwise harsh conditions (Cota-Sanchez and Abreu 2007), and larger viviparous seedlings may, subsequently, suffer lower mortality than smaller seedlings produced from seeds.

6.3 Growth and Survival

Seedlings and juveniles are the most vulnerable stage in most plants (Silvertown and Doust 1993). The usually slow growth rates of vascular epiphytes (Sect. 5.5.6) prompt the expectation of particularly long juvenile phases. Indeed, individual bromeliads or orchids are on average more than three times older at first reproduction (9.7 ± 4.5 years, $n = 17$ species, Table 6.1) than the typical terrestrial herbaceous plant (3.5 ± 3.1 years, $n = 63$ species, Moles et al. 2004). Twig epiphytes such as *Leochilus labiatus* or *L. scriptus* are enigmatic exceptions to the otherwise consistent picture of slow maturation in epiphytes (Chase 1986). Possibly the most stunning testimony of this accelerated life cycle is an observation by James D. Ackerman (Chase 1986). He found flowering *Ionopsis utricularioides* individuals on leaves of *Psidium guajava*!

Juvenile mortality seems mostly related to drought, as expected from theoretical considerations. Surface–volume ratios are inevitably larger in smaller plants compared to larger conspecifics, which increases the danger of desiccation, particularly during drier periods. This size dependence is well documented by two demography

Table 6.1 Time until first reproduction as an important life-history traits of vascular epiphytes. Data come from direct field observations or are estimates based on matrix model calculations or growth data. Estimates were either taken directly from the sources or calculated from published data. Also given are estimates for offshoots [*in brackets*]. Relative growth rates (RGR, in mg g^{-1} day^{-1}) are averages of 65 - 361 plants

Species	Family	Years to first reproduction	RGR	Source	Method
Aspasia principissa	Orchidaceae	10		Zotz and Schmidt (2006)	Matrix analysis
Catopsis sessiliflora	Bromeliaceae	6		Zotz and Laube (2005)	Estimates from field observations
Catopsis sessiliflora	Bromeliaceae	9		Winkler (2005)	Matrix analysis
Catopsis sp.	Bromeliaceae	9	3.3	Hietz et al. (2002)	Estimates from field observations
Dimerandra emarginata	Orchidaceae	6		Zotz (1998)	Estimates from field observations
Encyclia tampensis	Orchidaceae	15		Larson (1992)	Estimates from field observations
Jacquiniella leucomelana	Orchidaceae	6		Winkler et al. (2009)	Matrix analysis
Jacquiniella teretifolia	Orchidaceae	12		Winkler et al. (2009)	Matrix analysis
Leochilus labiatus	Orchidaceae	<1		Chase (1986)	Field observations
Leochilus scriptus	Orchidaceae	<1		Chase (1986)	Field observations
Lycaste aromatica	Orchidaceae	11		Winkler et al. (2009)	Matrix analysis
Tillandsia deppeana	Bromeliaceae	11	4.2	Hietz et al. (2002)	Estimates from field observations
Tillandsia deppeana	Bromeliaceae	9		Winkler (2005)	Matrix analysis
Tillandsia deppeana	Bromeliaceae	20		Matos and Rudolph (1984)	Field observations
Tillandsia deppeana	Bromeliaceae	[3]		Matos and Rudolph (1984)	Field observations
Tillandsia juncea	Bromeliaceae	15		Winkler et al. (2005)	Matrix analysis
Tillandsia juncea	Bromeliaceae	18	2	Hietz et al. (2002)	Estimates from field observations
Tillandsia multicaulis	Bromeliaceae	16		Winkler et al. (2005)	Matrix analysis

(continued)

Table 6.1 (continued)

Species	Family	Years to first reproduction	RGR	Source	Method
Tillandsia multicaulis	Bromeliaceae	13	2	Hietz et al. (2002)	Estimates from field observations
Tillandsia paucifolia	Bromeliaceae	8		Benzing (1981)	Estimates from field observations
Tillandsia punctulata	Bromeliaceae	8		Winkler (2005)	Matrix analysis
Tillandsia punctulata	Bromeliaceae	13	2.1	Hietz et al. (2002)	Estimates from field observations
Vriesea gigantea	Bromeliaceae	7–10		Trindade Sampaio et al. (2012)	Field observations
Vriesea gigantea	Bromeliaceae	[<5]		Trindade Sampaio et al. (2012)	Field observations
Werauhia sanguinolenta	Bromeliaceae	13		Zotz and Laube (2005)	Matrix analysis

Table 6.2 Causes of mortality in *Vriesea sanguinolenta* (in % per size class)

	Causes of death			
Size class	Drought	Herbivory	Substrate failure	Other/unknown
A1 (atmospherics < 2 cm)	51 ± 5	0	17 ± 6	31 ± 9
A2 (atmospherics ≥ 2 cm)	42 ± 4	0	26 ± 9	30 ± 8
T1 (tanks < 5 cm)	30 ± 8	0	35 ± 10	35 ± 9
T2 (tanks < 10 cm)	32 ± 7	6 ± 3	39 ± 8	23 ± 5
T3 (tanks < 20 cm)	20 ± 6	4 ± 3	51 ± 11	24 ± 4
T4 (tanks < 40 cm)	0	2 ± 1	45 ± 12	51 ± 11
T5 (tanks ≥ 40 cm)	0	0	83 ± 7	16 ± 7

The seven size classes are defined by size and morphology in this heteroblastic species (*A* atmospherics, *T* tank). "Substrate failure" is any disturbance that is related to the host tree, from flaking bark to tree fall. Data are means ± SE of 7 years. More details in Zotz et al. (2005)

studies in lowland Panama, which lasted for 7 years each (Table 6.2, Zotz and Schmidt 2006; Zotz et al. 2005). For example, in the orchid *Aspasia principissa* both growth and survival correlated with precipitation in smaller size classes, while larger individuals were completely unaffected. This lack of a response in larger epiphytes is quite remarkable, because the study period witnessed one of the driest years (c. 1400 mm a^{-1}) on record, and co-occurring trees have been shown to be strongly affected by such drought (Condit et al. 1995).

Epiphytes root on a living substrate with its own dynamic, and there is substantial evidence that "substrate instability," e.g., flaking bark, breaking branches, or even whole tree falls are the major reason for mortality in vascular epiphytes (Hietz 1997; Mondragón et al. 2004a; Zotz et al. 2005; Cabral et al. 2015), although juveniles may primarily die because of desiccation. It would be highly interesting to combine the demographic data of epiphytes with data on substrate demography. Unfortunately, this has never been tried. The generally slow development of both epiphytes and trees could discourage many researchers, but twig epiphytes may represent an ideal system for "short-term" studies of the race between an epiphyte to grow and reproduce before its short-lived substrate dies with its client (Cabral et al. 2015).

6.4 Reproduction

It has been suggested that epiphytes, due to the rather ephemeral nature of their substrate and their relatively small size, paired with frequently low population densities, should engage in inbreeding more often than terrestrial perennials (Bush and Beach 1995; Hooper and Haufler 1997). The available evidence only partly bears out this expectation. Although the majority of the tested Bromeliaceae and members of other families such as Gesneriaceae or Melastomataceae are indeed mostly self-compatible (Bush and Beach 1995; Matallana et al. 2010; Lumer 1980), the large majority of all studied orchids and ferns are obligate outcrossers. Self-incompatibility associated with pollinator limitation frequently led to extremely low fruit set under natural conditions, e.g., only c. 2 % of all flowers develop a fruit in *Tolumnia variegata* (Tremblay et al. 2005).

It is still difficult to generalize, however, because our knowledge of the mating systems in vascular epiphytes is highly biased. Most information is available for orchids (Tremblay et al. 2005; Ackerman and Montalvo 1990) and bromeliads (Matallana et al. 2010; Paggi et al. 2013), but only the exceptional study dealt with the topic in members of other important families, e.g., Araceae (Valerio and Villalobos 1980), Melastomataceae (Lumer 1980), Gesneriaceae (Bush and Beach 1995; Marten-Rodriguez et al. 2015), or ferns (Hooper and Haufler 1997).

Ackerman (1986) proposed three pollination strategies for outcrossing epiphytes, which he believed would ensure successful pollination, but supplied no quantitative comparisons of the prevalence of these strategies in epiphytic and terrestrial relatives. Similarly, Tremblay et al. (2005) provide an authoritative review of the mating systems of orchids, exploring, e.g., latitudinal differences in fruit set or the evolutionary consequences of small effective population sizes. Unfortunately, possible differences among epiphytic and terrestrial species were not addressed. Thus, it is still unresolved, whether a preliminary analysis by Neiland and Wilcock (1998), who found no differences in fruit set in terrestrial and epiphytic tropical orchids, is actually valid for this family at large, let alone other major epiphyte groups such as bromeliads (Paggi et al. 2013). Solid datasets for a number of different families such as the recent study of Marten-Rodriguez et al. (2015) with gesneriads are needed to address this question. A fine-scale tuning of the mating system to environmental gradients within tree canopies is suggested by the results of a comparative study in Mexico (Hietz et al. 2006). The observed trend toward higher inbreeding in species colonizing the outer, more dynamic portion of tree crowns is expected from ecological theory (Grime 1977).

In contrast to Benzing (2000), who assumed self-incompatibility to dominate in bromeliads, quantitative evidence for 40 species from the Atlantic rainforest indicates otherwise (Matallana et al. 2010): all 17 epiphytic Tillandsioids were self-compatible and 12 out of 23 epiphytic Bromelioids. A literature survey conducted by these authors indicated that the level of self-compatibility in epiphytic bromeliads is not really distinct from terrestrial species. For example, six of nine studied terrestrial species shared this character.

Many other aspects of reproduction have also been studied in epiphytes, e.g., the cost of reproduction (Zotz and Schmidt 2006; Ackerman and Montalvo 1990; see also Sect. 5.4.4), the specificity of pollinators (Tremblay et al. 2005), or the effect of spatial population structure on reproductive success (Murren 2002). Results do not indicate anything genuinely distinctive for epiphytes compared to terrestrial herbs. This is also true for the possible link of inbreeding and short-term demographic success of a species, similar to the situation in terrestrial pioneers. Several studies found a relationship of relative abundance and breeding systems that do not depend on pollinators. For example, *Tillandsia recurvata*, a bromeliad accounting for up to 90 % of all epiphyte individuals in a dry forest in Morelos, Mexico, is selfing (Orozco-Ibarrola et al. 2015), and so are the two orchids *Dimerandra emarginata* and *Caularthron bilamellatum*, which represent almost 60 % of all individual epiphytes in *Annona glabra* trees in the moist lowlands of Panama (Laube and Zotz 2007).

Many epiphytes do not only propagate sexually, but by vegetative means as well. For one, independent ramets simply result from the partial disintegration of creeping plants (e.g., in many ferns, gesneriads, or cacti), or the breaking apart of branches of rhizomes of sympodial orchids. Offshoots are another possibility to secure continuity of a genet, and in many monocarpic bromeliads, the production of offshoots is an integral part of their life history (Benzing 2000). Additional offshoots are also known for some orchids, where they form on stems or on flower stalks. These offshoots are well documented in the horticultural literature, but there is only one study addressing their importance in the field: Zotz (1999) studied their occurrence in the orchid, *Dimerandra emarginata*, in lowland Panama. Their relatively rare occurrence in 2 % of all individuals and low likelihood of establishment argue against an important ecological role.

6.5 Survival on the Ground

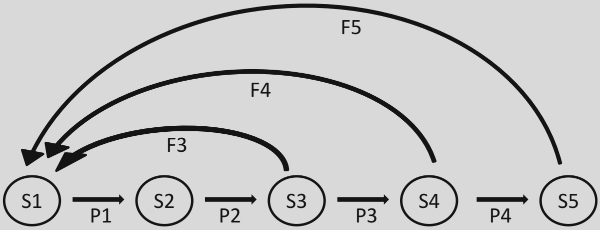
Falling *off* the substrate (e.g., with pieces of flaking bark) or falling *with* the substrate (e.g., in the case of branch or tree falls) are arguably the principal cause of mortality in larger epiphyte individuals (e.g., Hietz 1997; Mondragón et al. 2004a; Zotz et al. 2005). Three studies have directly tested the implicit assumption that continued existence on the forest floor is impossible by following the fate of epiphytes on the forest floor (Mondragón and Ticktin 2011; Matelson et al. 1993; Pett-Ridge and Silver 2002). The results were not entirely consistent: while most plants died very fast and few plants survived more than a year in two of the studies, survival on the ground was much higher in the study by Pett-Ridge and Silver (2002). These differences are certainly partly due to methodology. In contrast to the two other, purely observational studies, Pett-Ridge and Silver (2002) transplanted plants, which thus had not suffered possible damage during fall. Moreover, transplants were supported by PVC stakes, thus ensuring tank function, which would frequently not be the case in naturally fallen individuals. Nevertheless, counting all plants which fall off a branch in a demographic study as dead is probably an overestimate even for obligate epiphytes. I have repeatedly observed plants that got caught in and on lower branches, eventually attaching themselves with new roots and continuing to live there for many years (G. Zotz, unpubl. obs.). The notion of a “deadly” forest floor must also be qualified for many of the more flexible members of tree-dwelling flora. Many *Peperomias*, filmy ferns, etc., will easily trade bark for, e.g., rock as substrate as long as other abiotic conditions are conducive to survival. An example from the Fortuna Forest Reserve in Panama also indicates that at least some epiphytes can be quite opportunistic. Clearing of montane forest along the road has resulted in a low herbaceous-shrubby vegetation with little establishment of trees after more than a decade. A substantial number of epiphytes, e.g., orchids and bromeliads, are found vigorously growing on the ground. Similar observations have been made at forest margins or open ecotones such as the sub-Páramo.

6.6 Comparative Plant Demography

Detailed demographic information is available for about 30 species of epiphytes (Mondragón et al. 2015), equally representing orchids and bromeliads. The dynamics of individual plant populations is summarized by the ratio of the numbers of individual plants in successive years, the finite rate of population growth (λ). Both elasticities of vital rates (Franco and Silvertown 2004) and matrix element elasticities (see Box 6.2, Silvertown et al. 1993) have been used in comparative plant demography to analyze the relative contributions of different life-history components (fecundity, survival, growth) to λ, with very consistent results: Silvertown and Franco distinguished three groups (semelparous perennial herbs, iteroparous herbs, and woody plants) and discovered that these were usually found in distinct regions of the parameter space defined by fecundity, survival, and growth. These analyses included very few epiphytes (e.g., *Tolumnia variegata*, Calvo 1993), and not surprisingly, there was no attempt to distinguish epiphytes as a separate group. A considerable number of demographic studies with epiphytes published in the last decade now allow such an analysis (Fig. 6.1). With one exception, a study with *Tillandsia makoyana* (Martínez-García 2006), survival always influenced λ far more than growth (average $75 \pm 12\,\%$ vs. $21 \pm 10\,\%$, $n = 32$ species), let alone fecundity ($4 \pm 4\,\%$). Thus, these herbaceous vascular epiphytes resemble long-lived trees in their demography much more than iteroparous herbs rooted in soil. Noteworthy, there are several, albeit anecdotal, reports that individual plants in cultivation may reach ages well over 100 years (Smith 1966; Anonymous 1968).

Box 6.2 Population Matrix Analysis of an Epiphytic Orchid

Repeated census data of plant populations allow the construction of life-cycle graphs and so-called Lefkovitch matrices (for a detailed discussion of the topic please, refer to Caswell 2001). The figures below show a simplified life-cycle graph and a habit sketch of *Dimerandra emarginata*. Following the suggestions of Vandermeer (1978), five stages were recognized in this study (Zotz 1998 and previously unpublished data): S1–S5, plant size <2 cm, <5 cm, <10 cm, <18 cm, and ≥ 18 cm. Arrows depict possible contributions of an individual in stage i at time t to stage j at t +1, i.e., after one 1 year, either due to growth (P) or due to the production of progeny (F). Since only plants > 5 cm reproduce and a seedbank is lacking, additions to S1 come only from S3–S5.



The average data of three annual censuses (1993–1996) were used to produce a projection matrix (Table 1, $B = \{b_{ij}\}$, where $i, j = 1, 2, 3, 4$), which contains the transition probabilities and contributions (i.e., fecundity) of an average individual at different stages of the life cycle over a unit time interval, and operates over a vector (n_t) containing the distribution of individuals in the population.

The size of the entire population after one time interval is equal to the product of matrix B by vector n_t or

(continued)

Box 6.2 (continued)

$$N_{t+1} = B\, n_t.$$

The largest eigenvalue of this matrix (Table 1 below) is equivalent to the finite rate of increase of this population (λ), 0.99 in the shown example; i.e., the population is stable. Further analyses, e.g., an elasticity analysis (Table 2 below), allow the quantification of different demographic processes to λ. We distinguish (compare Silvertown and Doust 1993): stasis and retrogression (L, remaining in the same or lower stage class), growth (G, change into a higher one), or reproduction (F, recruitment of seedlings from current sexual reproduction). This approach quantifies the proportional change in λ resulting from an infinitesimal proportional change in a matrix transition a_{ij}. Importantly, elasticities of transitions of similar type can be added, and all elasticities of a transition matrix sum up to unity. This allows the comparison of the relative importance of different types of transitions between populations of the same species or among species (see Fig. 6.1). In the shown example L alone accounts for 73 %, while F is a mere 3 %.

Table 1 Average transition probability matrix for *Dimerandra emarginata* in the Barro Colorado National Monument

	Stage at year *t*				
Stage at year *t* + 1	S1	S2	S3	S4	S5
S1 (<2 cm)	0.37 ± 0.12	0.01 ± 0.01	0.05 ± 0.01	0.04 ± 0.03	0.27 ± 0.18
S2 (<5 cm)	0.25 ± 0.09	0.50 ± 0.05	0.07 ± 0.01	0.02 ± 0.02	
S3 (<10 cm)	0.03 ± 0.01	0.36 ± 0.12	0.54 ± 0.06	0.16 ± 0.02	0.02 ± 0.02
S4 (<18 cm)		0.04 ± 0.02	0.32 ± 0.10	0.61 ± 0.01	0.23 ± 0.06
S5 (≥18 cm)			0.03 ± 0.04	0.17 ± 0.01	0.70 ± 0.10
Mortality rate	0.35	0.04	0.05	0.04	0.06

The previously unpublished data are averages ±SD of three annual matrices. For more details, see Zotz (1998)

Table 2 Average elasticity matrix for *Dimerandra emarginata* in the Barro Colorado National Monument

	Stage at year *t*				
Stage at year *t* + 1	S1	S2	S3	S4	S5
S1 (<2 cm)	0.02	0	0	*0.01*	*0.02*
S2 (<5 cm)	**0.03**	0.05	0.01	0.01	0
S3 (<10 cm)	0	**0.04**	0.12	0.05	0.
S4 (<18 cm)	0	0	**0.08**	0.22	0.05
S5 (≥18 cm)	0	0	**0.01**	**0.07**	0.20

The previously unpublished data are averages of three annual matrices. Different styles indicate stasis and retrogression (L, remaining in the same or lower stage class: normal), growth (change into a higher one, **bold**), or reproduction (recruitment of seedlings from current sexual reproduction, *italics*)

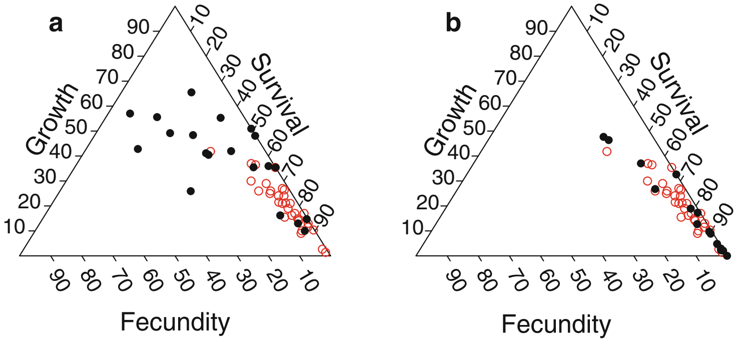


Fig 6.1 Comparison of the distribution of 32 epiphyte species (*open circles*) in the growth–survival–fecundity space with a) terrestrial herbaceous perennials and b) trees (*closed circles*). Studies with epiphytes were taken from the compilation of Mondragón et al. (2015) with additional data for *Dimerandra emarginata* (Zotz 1998), *Tillandsia multicaulis* and *T. punctulata* (Toledo-Aceves et al. 2014), and *Pachyphyllum hispidulum* (Zotz et al. 2014). Data of terrestrial plants are from Silvertown et al. (1993). When more than one transition matrix was available for a given species, averages were used

In analogy to these interspecific analyses, life-history components should also differ between populations of the same species (Franco and Silvertown 2004), but there are few such studies with epiphytes. For example, Zotz (2005) studied three populations of the epiphytic bromeliad, *Vriesea sanguinolenta*, along a precipitation gradient across the Isthmus of Panama. The results hardly met expectations. Although population growth rates increased with precipitation, mortality rates being highest at the dry end and growth being highest at the wet end, the differences in the importance of the three demographic processes growth, survival, and reproduction for population growth were rather small.

As emphasized by Mondragón (2011), such demographic studies do not only answer basic scientific questions, but provide important information for management plans in conservation. Particularly in those regions, in which plants are collected in large numbers (Chap. 10) as non-timber forest products with an obvious economic importance, such management plans are essential for a sustainable use. First suggestions for such long-term management are now available (Mondragón and Ticktin 2011; Wolf 2010).

6.7 Metapopulations

Metapopulations are populations of populations which are interconnected by seed dispersal, and metapopulation models focus on the importance of colonization and extinction processes for regional dynamics rather than local processes (Hanski and Gaggiotti 2004). Overton (1994) was the first to apply the concept of metapopulations to plants anchored on trees. Although he studied parasitic mistletoes, these are comparable to true epiphytes in this regard because both groups are spatially structured into individual populations on trees (=“islands”) separated from other trees by a “sea” of inhospitable substrate. While there is debate on the applicability of metapopulation theory to plants in general (e.g., Freckleton and Watkinson 2002), epiphytes make ideal candidates for showing metapopulation structure. All four conditions specified by Hanski and Gaggiotti (2004) are actually met: (1) suitable habitats occur in discrete patches (=the individual tree) that may be occupied by local populations, (2) even large local populations have a measurable risk of extinction (branch or tree fall), (3) habitat patches are usually not too isolated to prevent recolonization following local extinctions, and (4) local populations do not have completely synchronous dynamics. A number of studies with vascular and nonvascular epiphytes during the last decade using a metapopulation approach (e.g., Snäll et al. 2003; Tremblay et al. 2006; Laube and Zotz 2007; Winkler et al. 2009) have considerably increased our database and also provided important conceptual advances. Snäll et al. (2003) introduced the patch-tracking model, which describes the relationships of epiphytes and trees much better because the dynamics of the tree are included appropriately. First, trees (=potential hosts) establish, but colonization by epiphytes may be delayed (possibly for decades, compare Zotz and Vollrath 2003). After initial colonization, species abundance will normally increase with time, and the population will eventually become an increasingly important regional source of propagules. In a pure patch-tracking model, extinctions (=tree falls) are independent of epiphyte occurrence or abundance, but Snäll et al. (2003) rightfully pointed out that their model should not be used typologically, but rather as an endpoint of a gradual change in the relative importance of key processes from classical metapopulation models to their patch-tracking model.

Metapopulation models may be particularly useful in situations with a high degree of host specificity (Sect. 7.2), or in fragmented landscapes, e.g., when epiphytes grow on scattered trees in pastures (Poltz and Zotz 2011). Snäll et al. (2005) analyzed the epiphytic lichen *Lobaria pulmonaria*, which is only found on aspen (*Populus tremula*) and goat willow (*Salix caprea*). Since these trees can only establish after forest fires and are subsequently replaced by conifers, regional dynamics of *Lobaria pulmonaria* depend strongly on fire frequency.

It is much less clear whether a metapopulation approach is always indicated and preferable to a classic population study for epiphytes in a continuous forest with possibly little or no host specificity, yet the answer to this question is clearly crucial when interpreting the data of population studies. For example, it has been suggested that the frequent observation of negative population growth rates ($\lambda < 1$) in epiphytes (compare Mondragón et al. 2015) may result from inappropriate averaging of the dynamics of subpopulations (Winkler et al. 2009). In other words, are regional dynamics primarily determined by regional processes (immigration, emigration), while local processes are largely irrelevant? Winkler et al. (2009) directly addressed this question by analyzing their dataset of three epiphytic orchids from a montane forest in Mexico with (a) average stage-classified transition matrices and (b) with metapopulation matrices. Indeed, population growth rates were consistently below unity in the former and slightly above unity in the latter. Elasticity analysis revealed, however, that the most important process in both models was individual survival, i.e., a local process. This suggests that local demographic processes are important at the regional level, and results from classic demographic studies can be used in a meaningful way to deduce the dynamics at larger scales.

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Epiphyte Communities

7

Community ecology is concerned with the inventory of “local, potentially interacting assemblages of species” (Crawley 1997), the study of spatial and temporal variability of their species composition or differences in abundance, as well as the exploration of the underlying processes. Although Clements’ (“communities as superorganisms”) and Gleason´s (“communities as random assemblages of individual species”) classic views on the theoretical foundations of community ecology are still treated as a starting point in many modern textbooks, we have certainly moved on, acknowledging the roles of both abiotic and biotic factors and, last but not least, chance (Crawley 1997). In spite of many contentious issues in the study of “communities” (e.g., their usually vague spatial delimitation, Crawley 1997), the concept is probably here to stay (see Ricklefs 2008 for a critique).

The application of the community concept to epiphytes causes an immediate problem. By depending structurally on other plants, epiphytes are only *part* of a local plant community and cannot form separate “plant communities” in the strict sense, and some researchers, e.g., Barkman (1958), Grubb et al. (1963), or Richards (1996), proposed the use of the term synusia for studies with epiphytes. This is not entirely appropriate either because this term is typically used for a group of plants that occupy the same layer in a vegetation stand with similar microenvironmental conditions, e.g., ground-layer herbs (van der Maarel 2005). Thus, the use of synusia is incompatible with the substantial vertical gradients experienced by epiphytes in local assemblages (Sect. 5.1).

The term “epiphyte community” is well established in the literature (e.g., Wolf 1993; Hietz and Hietz-Seifert 1995; Johansson 1974) and, although not entirely correct, its continued use should not cause any conceptual confusion, although the use of the term “assemblage” may be more appropriate (Mendieta Leiva and Zotz 2015). Irrespective of these terminological issues, epiphytes are actually particularly suited for an analysis as distinct spatial units, i.e., all epiphytes on a given tree (“tree-based assemblage” sensu Mendieta Leiva and Zotz 2015), because such a unit of analysis avoids the usual vagueness of the spatial delimitation of a plant

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community. Analytically, such an assemblage can be easily scaled down ("zone-based assemblage" sensu Mendieta Leiva and Zotz 2015) or scaled up ("metacommunity" or "stand-based assemblage" sensu Mendieta Leiva and Zotz 2015).

There is a growing body of reports on the composition of vascular epiphyte communities (reviewed in Mendieta Leiva and Zotz 2015, Box 7.1), but most studies suffer from what Kitching (2006) deplored as paucity of theory. This contrasts with the theory-driven approach of most community ecologists working with tropical trees. Over the last decades, tree ecologists have tested a range of hypotheses for community assembly; e.g., they worked in the framework of the pioneer/late successional continuum (Sheil 2001; Dalling et al. 1998), the Janzen-Connell theory (Janzen 1970; Gilbert et al. 1994; Bagchi et al. 2014), or Hubbell's neutral theory (Hubbell 2001; Condit et al. 2006). This research has led to an impressive progress in our understanding of the assembly of these hyperdiverse tree communities (e.g., Rosindell et al. 2011; Kraft et al. 2008; Condit et al. 2000, 2002). In contrast, many studies of epiphyte communities do not go beyond an enumeration of species and individual numbers at a particular locality or at best a test of, say, the relationship of tree size and epiphyte diversity. There is no doubt that such work is very valuable for local conservation purposes and that results are useful as baseline data on the biogeography and ecology of species and possibly the starting point for long-term studies, but it is currently hard to impossible to connect these studies within a larger theoretical framework.

Box 7.1. Sampling Epiphyte Communities

Sampling epiphyte communities causes unique problems because of their three-dimensional distribution, with difficult access in all but small-statured forests via single-rope or double-rope climbing, canopy cranes, or other canopy-access systems (compare Box 2.2). The alternative, i.e., observations from the ground, yields biased results at least in dense forests, where species are easily missed, particularly the smaller and inconspicuous ones (Flores-Palacios and García-Franco 2001; Burns and Dawson 2005). A number of papers have suggested appropriate methodology to document epiphyte diversity and community structure (complete list of studies in: Zotz and Bader 2011), but considering the many forest types and the multitude of research questions, it is probably vain to ask for a single, standardized methodology. Yet in order to be a useful contribution for future meta-analyses, it seems essential to make every effort to obtain a representative description of the studied epiphyte community in terms of species diversity and community structure and provide at least some minimum information on host trees (Mendieta Leiva and Zotz 2015).

A surprisingly small sample may suffice for a fair representation of the local species pool and relative abundances (Zotz and Bader 2011; Gradstein

(continued)

Box 7.1 (continued)

et al. 2003). A sample of the epiphytes in 8 large trees in a local lowland plot, which had been censused extensively with the help of tower crane (Zotz and Schultz 2008), yielded a satisfactory description of the structure of a species-rich epiphyte community in terms of (a) the total species number, using richness estimators, (b) α-diversity, and (c) evenness. Even relative species ranks were very similar to those of the entire census of 0.4 ha of lowland forest. However, these findings may not be transferable to other forests. In montane sites in Bolivia, Krömer et al. (2007) identified a large number of epiphyte species on small trees that were not found at all on larger trees. Moreover, a sample size of 8 trees will hardly be enough to ask questions about the roles of host species identity and the effect of tree size or provide any insights into spatial patterns. You cannot be fast and comprehensive!

An issue of fundamental importance in any community study is the definition of “epiphyte.” Lacking a real consensus, “epiphyte” studies may include only holo-epiphytes, but also mingle these with hemiepiphytes, nomadic vines, or even mistletoes. The frequent practice of lumping these life forms in a single analysis is quite problematic in view of their very different ecologies, and makes later comparisons among studies difficult to impossible, particularly when authors do not specify life form in their species lists. On the other hand, studying structurally dependent flora, i.e., vascular epiphytes, nonvascular epiphytes, hemiepiphytes, mistletoes, vines, and lianas in a comparative way at the same site (compare, e.g., Kelly et al. 2004; Burns and Dawson 2005), may only be encouraged and may produce important insights into possible positive or negative interactions between co-occurring, structurally dependent life forms.

There were a few attempts to label units of epiphyte vegetation using the syntaxonomic system of the Braun-Blanquet school (Braun-Blanquet 1964), for example Alves et al. (2008). Considering the enormous species richness of tropical forests, it is doubtful that species-based categorizations of epiphyte communities are really useful to reach general conclusions. A more complicated classification scheme, which distinguishes several life forms among epiphytes, was introduced by Hosokawa (1968) and would potentially allow a more functional interpretation of species composition and also species-independent comparisons of different studies. This scheme has rarely been applied by other authors (e.g., Freiberg 1996), and its usefulness for large-scale comparisons remains largely untested.

Unfortunately, we cannot simply borrow from studies with other life forms such as trees and transfer the many insights obtained for trees to epiphytes. While biotic interactions (e.g., competition or pathogen/herbivore pressure) are of major importance for the structure and dynamics of tree communities, these processes seem to play a minor role in most epiphyte communities (Zotz and Hietz 2001). Epiphyte ecology is also inherently three-dimensional, and community structure is strongly influenced by vertical gradients in abiotic conditions, but also by horizontal gradients, e.g., from inner crown (shaded, older, less dynamic) to outer crown (more exposed, younger, more dynamic). The inherent structural dependence implies that epiphytes are also strongly affected by (1) the structure of the forest, i.e., the spatial distribution of trees and the three-dimensional structure of each tree, and (2) the dynamics of this habitat, e.g., the frequency of tree and branch falls (Hietz 1997; Cabral et al. 2015).

There is good reason to expect this situation to change substantially in the future because there have been several recent attempts to improve the theoretical basis of research on epiphyte community ecology. Burns (2007), Blick and Burns (2009), and Burns and Zotz (2010) have introduced a network and a metacommunity approach to the analysis of epiphyte communities (Fig. 7.1). The great potential of network analysis for a functional understanding of community structure, particularly in combination with data on the host trees, was demonstrated in a subsequent study by Sáyago et al. (2013). These authors were able to show a positive association of epiphyte abundance with tree characteristics, in particular wood density and bark texture. Sáyago et al. (2013) provide a mechanistic interpretation of these associations: rougher bark improves both attachment and moisture supply, while wood density improves branch stability. More recently, Mendieta Leiva and Zotz

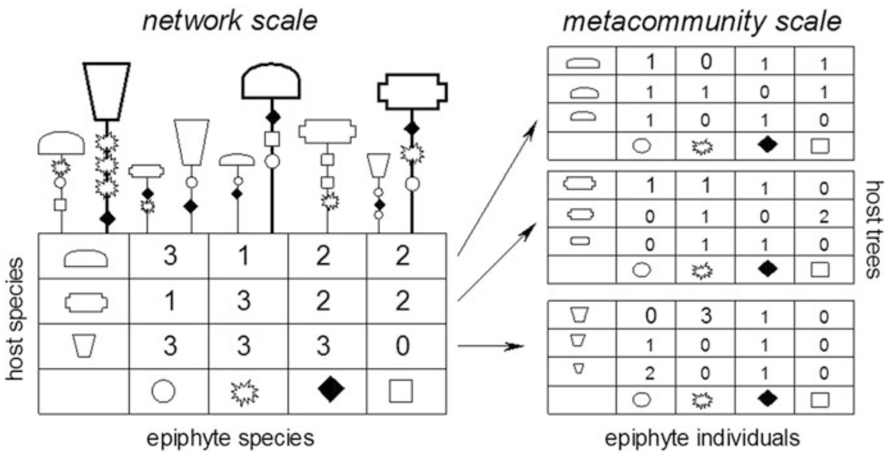


Fig. 7.1 Schematic illustrating the meta-network analytical framework of Burns and Zotz (2010). The *left-hand column* shows an epiphyte–host species interaction network consisting of three host species, each of which is represented by three trees, and four epiphyte species. The illustrated hypothetical epiphyte community in this forest corresponds to an interaction matrix whose entries are the interaction frequencies of each species pair. A different approach analyzes all epiphytes on a given host tree species as a metacommunity. The resulting three epiphyte metacommunities, which are merged into single rows in the network matrix, are shown in the *right-hand column*. Reproduced with permission from Burns and Zotz (2010)

(2015) presented a somewhat different analytical framework to that of Kevin Burns and coworkers. They emphasized the distinction of different ecological scales, from epiphyte assemblages in a given zone on a tree, on entire trees to assemblages of epiphytes on assemblages of trees (=stands). By (re-)analyzing published and unpublished data, they showed that conclusions on differences in diversity patterns of vascular epiphytes in comparative studies depend on scale. They advocate a consistent methodology, the collection of a minimum amount of information on the host trees in every epiphyte study, and finally make a plea to make data available for meta-analyses. To conclude, adopting the theory-driven approach of tree ecologists and joining forces by sharing data should lead to major advances in our understanding of epiphyte community ecology.

Lack of theory is less of an issue in those studies which address the *abiotic* determinants of epiphyte community structure (Fig. 7.2). Previous ecophysiological work with a wide range of terrestrial plant species (Lambers et al. 2008) allows us to make clear, testable predictions of how plant traits will vary with height in the forest or in forests varying in macroclimatic conditions. An example of an early application of such an approach is the study by Griffiths and Smith (1983) that built on a descriptive study by Pittendrigh (1948), a classic in epiphyte ecology. Griffiths and Smith (1983) were able to correlate the distributional patterns identified by Pittendrigh (1948) with the occurrence of CAM, both in regard to higher exposure

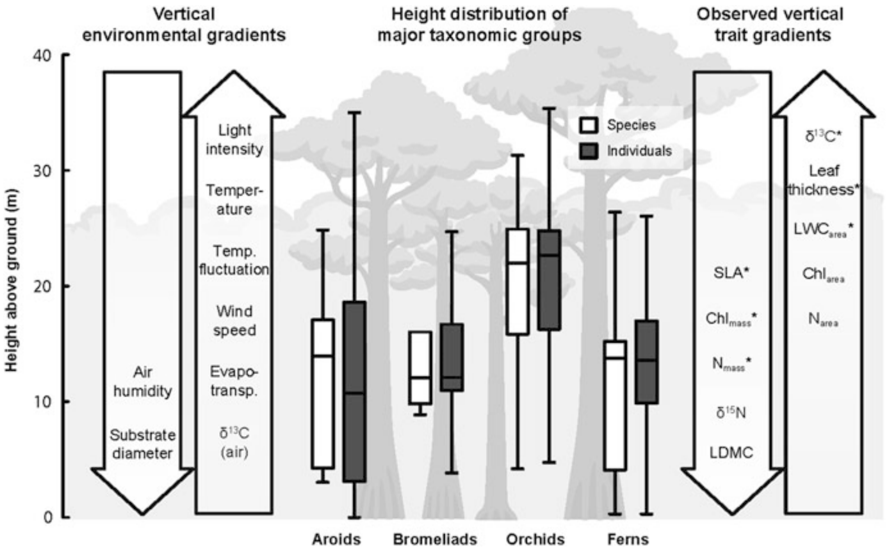


Fig. 7.2 Vertical distribution of environmental factors, plant traits, and taxonomic groups of epiphytes in a wet lowland forest in Panama. Height distributions of major taxonomic groups are based on (1) the height of all individuals or (2) the mean height of each species: *horizontal lines* in the *boxes* represent median heights, *boxes* interquartile ranges, and whiskers 95 % confidence intervals. Leaf traits showing pronounced changes in community trait means with height are marked with an *asterisk*. Reproduced with permission from Petter et al. (2016)

within a forest and to the occurrence in increasingly drier vegetation. Subsequent work has studied variation in a large number of important plant traits within a forest (e.g., Hietz and Briones 1998; Parra et al. 2009) and between forests (e.g., Earnshaw et al. 1987), but there are still many unused research opportunities. I refer the reader to Chap. 5 for a detailed account on epiphyte ecophysiology in which such opportunities are identified.

7.1 The Host Tree

By definition, epiphytes are physically dependent on a host, which immediately suggests an important role of the host tree for the structure and dynamics of epiphyte communities. Since the publication of Schimper's seminal work in 1888, over 200 papers have touched the issue of "host preference" or "host specificity" in vascular epiphytes (Wagner et al. 2015). Unfortunately, few of these studies such as Laube and Zotz (2006b), Fig. 7.3) use statistical analyses within a rigorous theoretical framework. Wagner et al. (2015) recently developed such a framework in considerable detail (Fig. 7.4). This scheme defines various types of host specificity that should guide future research and hopefully will eliminate the current terminological confusion. Particularly useful is the distinction between "basic host specificity," which refers to the potential interaction of epiphyte and tree species, and "structural host specificity," which refers to differences in the performance of an epiphyte on different hosts.

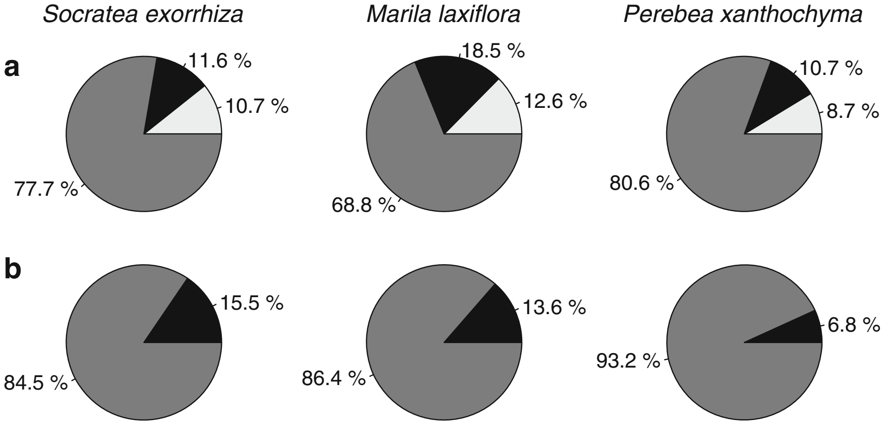


Fig. 7.3 Host bias in epiphytes. Occurrence of epiphytes on three tree species and null model expectations. (**a**) Individual-based comparisons and (**b**) tree-based comparisons. Data are from the San Lorenzo forest plot in Panama. *Gray*: frequencies indistinguishable from random; black: species found with, respectively, more individuals or on more trees than expected, white: species found with fewer individuals on a host tree species than expected by chance. Modified after Laube and Zotz (2006b)

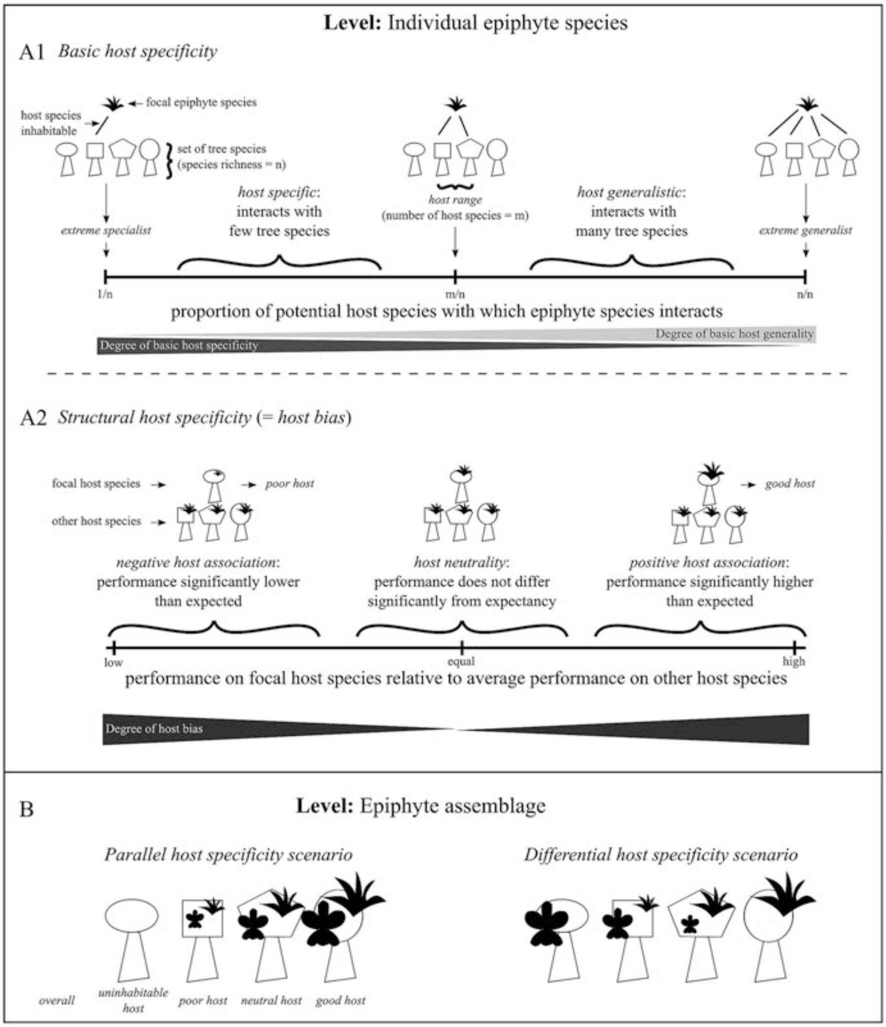


Fig. 7.4 Conceptual framework for epiphyte–host interactions in vascular epiphytes (*A*1) "basic host specificity" analyzes the proportion of tree species inhabitable by a *focal epiphyte species* and (*A*2) "structural host specificity" addresses the relative performance of a *focal epiphyte species* on different tree species. An integrative approach identifies host biases at the *epiphyte assemblage* level (*C*). Reproduced under creative commons licence from Wagner et al. (2015)

Noteworthy, ecological theory does not predict strong interactions between epiphytes and their hosts because their relationship is generally considered to be basically commensalistic. This contrasts with other types of species interactions that are much more likely to lead to specificity. Co-evolution is expected both in antagonistic (e.g., in plant–herbivore systems because of an "arms race," Ehrlich and Raven 1964) and in mutualistic systems, e.g., between plants and pollinators, because plants should respond to specialist pollinators that are more effective than generalists (Blüthgen et al. 2007). Nevertheless, current evidence suggests that a certain host bias is ubiquitous in epiphytes (Wagner et al. 2015). However, the case for *extreme* host specificity ("extreme basic specificity," Fig. 7.4) is very weak. Although there are > 20 reports of extreme basic specificity in the literature, only two of these provide quantitative data (Alves et al. 2008; Tremblay et al. 1998). All other claims can be found in species descriptions and/or are purely observational. It is telling that later evidence showed that the claim of host specificity was premature in one of the two mentioned cases (Crain and Tremblay 2012).

To conclude, there is a large body of empirical evidence on host bias, but due to inconsistency in terminology and to a number of inherent methodological problems in hyperdiverse tropical forests (compare Wagner et al. 2015), we are still far from a satisfying quantification and generalization of the importance of host biases for the structure and dynamics of epiphyte assemblages.

7.1.1 Host Tree Identity

The suitability of a particular host species for epiphytes is not caused by its "Latin binomial" (Raffaelli 2007) but rather by the matching of host and epiphyte traits. Important host traits relate to tree architecture (branching patterns, branch size distributions, branching angles) and physical and chemical bark characteristics (stability, texture, water-holding capacity, chemistry), but also species-specific growth rate and maximum size as well as leaf phenology. It is important to note that many of these traits are not species constants, but change during ontogeny, which introduces another, temporal level of complexity to the interaction of epiphyte and tree (e.g., Taylor and Burns 2015).

Some host tree types have been mentioned repeatedly as particularly suited, or unsuited, for epiphytes. Tree ferns are an example of the former (Fig. 10.6, Sanger and Kirkpatrick 2014; Pope 1926) and needle-leaved conifers of the latter (Fig. 10.6, Guerrero-Hernandez et al. 2014, Kolbek 1995). Incidentally, pieces of tree fern trunks are frequently used to mount, e.g., epiphytic orchids in cultivation, which testifies to their suitability as substrate. Surprisingly, however, even in these well-documented cases there is little experimental work to identify the actual underlying mechanism (Dematte and Dematte 1996).

7.1.2 Host Tree Size

Individual trees are often described as the minimum habitat unit of epiphytes (e.g., Flores-Palacios and García-Franco 2006). This is certainly a valid concept in the case of isolated trees in pastures, but more problematic in continuous forest. There, epiphyte populations on immediately adjacent branches of neighboring trees may interact by exchanging pollen and seeds much more readily among each other than

Fig. 7.5 Drought deciduousness in epiphytes. Relatively few vascular epiphytes shed their leaves during the dry season. Drought deciduousness as a trait is, e.g., common among Catasetinae like this flowering *Mormodes* sp. The small leaves belong to a different species (*Codonanthe* sp.). (Photograph: Marcos Guerra)

with conspecifics growing on the other side of the crown of the same host, e.g., in the case of a large emergent. Acknowledging this limitation, island biogeography still represents a useful concept for the study of epiphyte communities. However, in contrast to most cases, trees continuously increase in size over time. The "general dynamic model of oceanic island biogeography" (Whittaker et al. 2008) provides a theoretical framework for dynamic islands, but this particular framework is hardly applicable to the temporal and spatial scale of trees and epiphytes. Thus, the insular habitat of epiphytes still awaits an appropriate theoretical treatment.

Typically, a positive relationship between epiphyte abundance and species richness and tree size is reported (Fig. 9.1, Flores-Palacios and García-Franco 2006; Zotz and Schultz 2008, but see, e.g., Boelter et al. 2011). This may indeed reflect a time effect, if epiphytes are severely dispersal limited or, alternatively, represent a size effect or a combination of the two. Larger trees make larger targets and also offer new microhabitat types (e.g., large horizontal branches) and an increased diversity of microhabitats (Woods et al. 2015). Large, old trees also

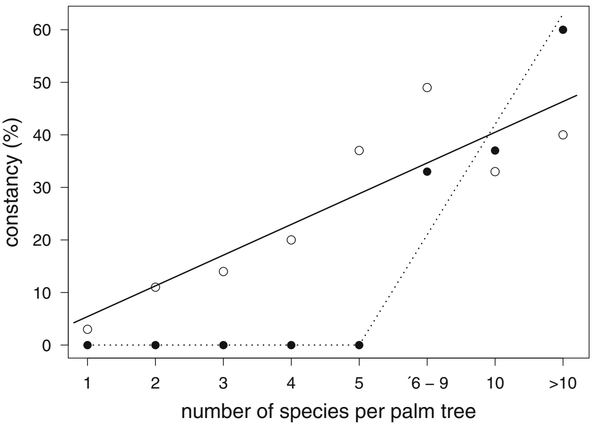


Fig. 7.6 Tree growth and epiphyte community dynamics. The majority of species show a continuous increase in constancy on larger and older trees of the palm *Socratea exorrhiza* with more species-rich epiphyte communities (e.g., *Dicranoglossum panamense*, *open symbols*). Heliophile species like *Niphidium crassifolium* (*closed symbols*) do not find appropriate growth conditions on small palms, but there is a similar increase in constancy once the host has reached higher strata of the forest. Modified after Zotz and Vollrath (2003)

encompass greater environmental heterogeneity from forest floor to upper forest canopy and are also likely to possess, e.g., more dead wood, which can be utilized by dead-wood specialists such as *Catasetum* spp. or *Mormodes* spp. (Fig. 7.5).

Many authors speculate on the actual mechanisms of host specificity, but few provide the necessary quantitative evidence. Zotz and Vollrath (2003) showed that growth in the palm *Socratea exorrhiza* can be seen as a vertical movement of new "substrate" through the forest with time, and light-demanding epiphyte species such as *Niphidium crassifolium* will not become established before the individual palm reaches a certain height which goes along with appropriate microclimatic conditions (Fig. 7.6). Another study also documents a direct size effect, but for another reason (Laube and Zotz 2007). Since the host tree *Annona glabra* is rather small and is always growing in the open, a microclimatic explanation for generally higher colonization in larger trees between two censuses can be excluded. Rather, an increased target size for diaspores is suggested. In contrast, Snäll et al. (2003) did not find a strong effect of tree diameter on colonization of epiphytic bryophytes and stressed the importance of time. In the end, both time and size are likely to play a role for colonization in most systems, but their relative importance is likely to vary from case to case.

7.1.3 Host Tree Phenology

Host trees shedding their leaves in the dry season exacerbate already demanding conditions for resident epiphytes, although some xerophytic cacti (Andrade and

Nobel 1997; Cardelús 2007) and bromeliads (Cardelús 2007; Birge 1911) may actually benefit. Most mesic epiphyte species, however, should be negatively affected by drought deciduousness of the host. In their detailed analysis of epiphyte assemblages on drought-deciduous, semi-deciduous, and evergreen tree species in moist lowland forest on Barro Colorado Island, Einzmann et al. (2015) demonstrated that epiphytes on drought-deciduous vs. evergreen trees differed in physiology, demography, and community composition. Differences were partly related to intraspecific variability in traits such as specific leaf area (SLA) or isotope ratios ($\delta^{15}N$), partly due to shifts in dominance of species (e.g., changes in the relative abundance of C3 and CAM species) and, to a smaller degree, species turnover: epiphyte species growing on deciduous trees were by and large also found on evergreen trees. Remarkably, leaf phenology affects epiphyte assemblages even when the deciduous phase occurs during the rainy season in wet forests, as reported by Cardelús (2007). This suggests that the mechanistic link between tree phenology and epiphyte species composition is not exclusively caused by severe water shortage, but is also due to more subtle effects on plant water relations, differences in light regimes, and possibly other microclimatic variables.

7.2 Community Composition and Structure

There are a considerable number of published local inventories of vascular epiphytes, with at least 60 of these going beyond simple species lists by reporting abundance estimates, i.e., the number of individuals per species (reviewed in Mendieta Leiva and Zotz 2015; for a review of methodologies, see Box 7.1). Epiphyte diversity has been documented at different scales, from point diversity (reference: single tree) to local diversity (reference: plot) to regional diversity (a series of plots along environmental gradients, regional species lists, and floras). The highest number of epiphyte taxa on a single tree ever reported is 190 species in a cloud forest in Peru (Fig. 7.7, Catchpole and Kirkpatrick 2010). This number is really exceptional considering that the second and third highest reports "only" list 126 (Costa Rica) and 83 species (Bolivian). A study from Mexico (Valdivia 1977) is often cited incorrectly in this regard—the number of 107 epiphyte species in *Ceiba pentandra* refers to the species number on *three* conspecific trees.

A review of species numbers and typical proportions of major taxonomic groups at the plot level in both the tropics and the temperate zones has already been presented in Chap. 3 (Fig. 3.5 and Table 3.1), and a selection of typical habitats is shown in Figs. 7.8. and 7.9. Probably more instructive than a detailed analysis of the taxonomic composition of epiphyte communities is the analysis of differences in ecologically relevant traits. For example, the occurrence of CAM is clearly associated with growth in drier vegetation types. Only about 25–35 % of the epiphytic orchid species in New Guinean, Australian, and Panamanian lowland rainforests use this photosynthetic pathway (Winter et al. 1983; Earnshaw et al. 1987; Zotz 2004), about 40 % of all

Fig. 7.7 Outstanding point diversity. This 32 m tall emergent *Ficus crassiuscula* in a Peruvian cloud forest is host of a stunning 190 species of vascular epiphytes (Catchpole and Kirkpatrick 2010). Views of the tree crown from inside (**a**) and outside (**b**) (Photographs: Damian Catchpole)

species use CAM in a moist forest in Panama (Zotz and Ziegler 1997), while this proportion reaches 100 % in dry forests (Mooney et al. 1989). Similar analyses can be conducted for other traits, e.g., one can compare the prevalence of bromeliads with an atmospheric habit with that of water-impounding tanks at local (Reyes-García et al. 2008) or regional scales (Gilmartin 1983).

Struggling with the appropriate description of the three-dimensional spatial structure of epiphyte communities, I chose an approach that has been used before several times in individual studies (e.g., Nieder et al. 2000; Zotz and Schultz 2008): I distinguish a vertical and a horizontal dimension, which are discussed successively. A three-dimensional analysis and visualization of spatial distributions is possible in systems with low abundances (e.g., the epiphyte community at Surumoni, Venezuela, Fig. 7.10, Schmit-Neuerburg 2002), but appropriate analysis tools for complex, individual-rich communities still need to be developed. With this two-step approach, the reader will hardly get a feel for a real epiphyte community. Therefore, as a specific example, the epiphyte community at the San Lorenzo Crane site in Panama is described in considerable detail in Box 7.2.

Fig. 7.8 Epiphyte communities in the temperate zones are usually dominated by ferns, and accidental epiphytes are common. The four examples cover important epiphyte hot spots in the temperate regions of the Northern and Southern Hemispheres. (**a**) A *Thuja plicata* tree in Vancouver Island (Canada, 48°N, 125°W) with one holoepiphytic fern (*Polypodium glycyrrhiza*) and many accidentals (Burns 2008), (**b**) a dense population of *Polypodium vulgare* on an oak tree in Killarney (Ireland, 52°N, 9°W), (**c**) lush epiphyte vegetation in a Valdivian forest near Huinay (Chile, 42°S, 72°W) with large flowering bromeliads (*Fascicularia bicolor*), (**d**) a similarly rich epiphyte community dominated by *Astelia solandri* on *Elaeocarpus dentatus* in Otari-Wilton's

Fig. 7.9 Epiphyte communities in the tropics. (**a**) Treeline with small-statured trees (Volcán Barú, Panama at 3400 m a.s.l.), (**b**) montane rainforest (Fortuna, Panama, ca 1200 m a.s.l), (**c**) Cerrado (Brazil), (**d**) moist lowland forest (Barro Colorado Island, Panama), (**e**) mangrove stand (Brunei), (**f**) inundated stand of *Annona glabra* (Barro Colorado Island, Panama). (Photographs (**c**) Gerhard Gottsberger, (**d**) Helena Einzmann, (**e**) Ulmar Grafe, (**f**) Moritz Klose)

Fig. 7.8 (continued) Bush (New Zealand, 41°S, 175°E). (Photographs: (**a,d**) Kevin Burns, (**b**) Moritz Klinghardt, (**c**) Simon Pfanzelt)

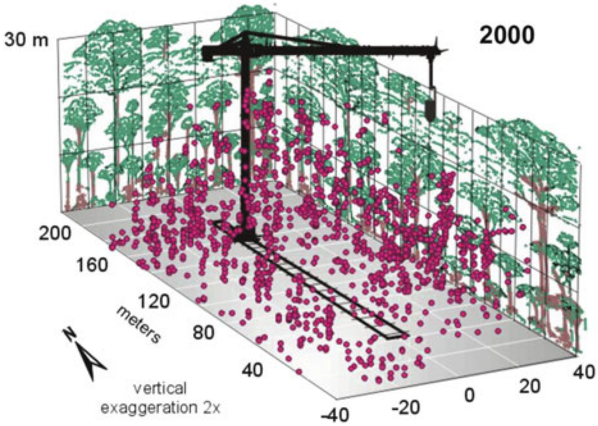


Fig. 7.10 Spatial distribution of epiphytes at the Surumoni Crane Plot in the year 2000 (Schmit-Neuerburg 2002). Each *dot* represents one individual epiphyte or a nomadic vine. Note that *dots* may overlap. Reproduced with permission from Schmit-Neuerburg (2002)

Box 7.2. The San Lorenzo Crane Plot

(Gerhard Zotz, Glenda Mendieta-Leiva, and Katrin Wagner)

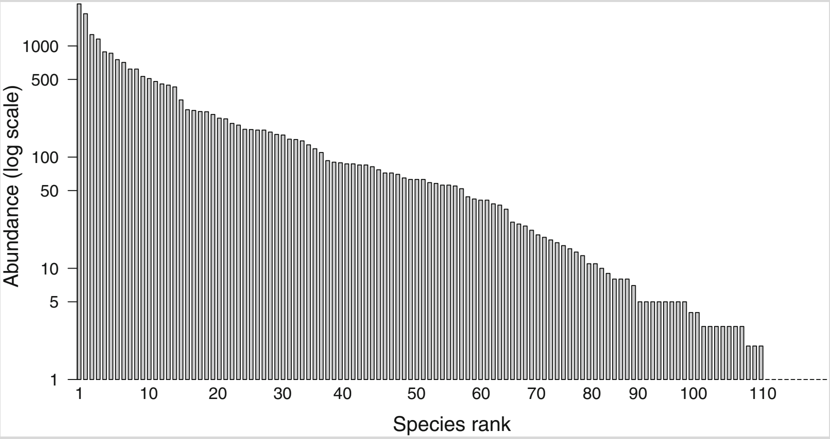
Descriptive and experimental long-term studies with plant communities are an essential tool for ecologists (Rees et al. 2001). Permanent vegetation plots have produced an enormous wealth of data that have allowed us to test important hypotheses concerning community structure and dynamics in systems as diverse as temperate grasslands (Silvertown et al. 2006) and tropical tree assemblages (Condit et al. 2005). In comparison, very few attempts of long-term monitoring of vascular epiphyte communities have been made. To our knowledge, there are only three *active* plot systems with repeated censuses globally: (1) a lowland rainforest on the Caribbean slope of Panama (the "San Lorenzo Crane plot," c. 1 ha with 3413 trees (174 species) with a diameter at breast height (dbh) > 1 cm, 2 censuses in 10 years, last one in 2012), (2) monotypic *Annona glabra* stands along the shores of Barro Colorado Island, Panama (c. 1200 trees with dbh > 1 cm, 3 censuses in 23 years, last one in 2015), and (3) pasture trees on the Pacific slope of Panama (c. 700 trees with a dbh > 10 cm, 2 censuses in 8 years, last one in 2013).

Here, we describe the epiphyte community at the San Lorenzo crane plot. In total, 20721 individuals out of 118 species were found in the second census. A rank-abundance plot shows a pattern typical for species-rich plant communities (McGill et al. 2007), with relatively few very common species

(continued)

Box 7.2 (continued)

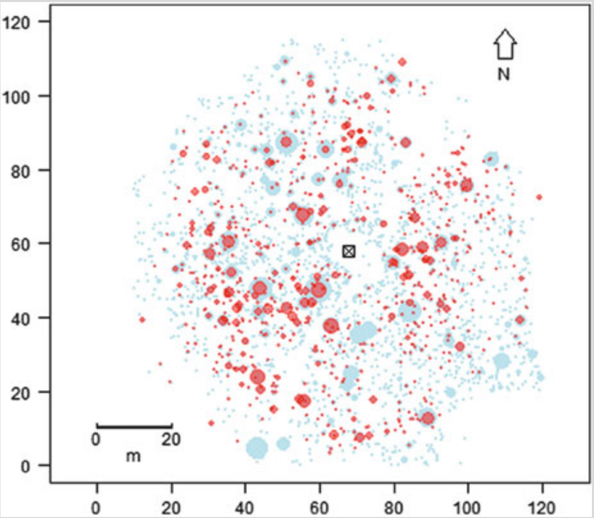
(e.g., *Ananthacorus angustifolius* or *Scaphyglottis longicaulis* with more than 1000 individuals in 2012) and many rare species: 30 species (e.g., *Heterotaxis sessilis* or *Lockhartia pittieri*) were found with 1–5 individuals. The following graph shows the species abundance distribution of all 118 species of the epiphyte community at San Lorenzo.



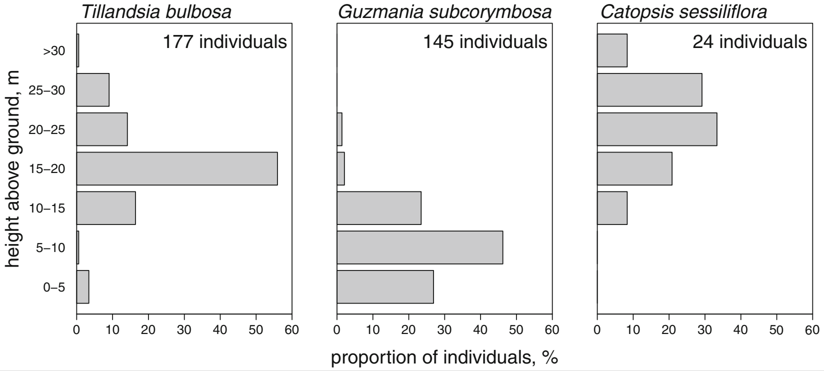
The detailed map below shows the distribution of trees and epiphytes in 2012. The gray circles represent individual trees (size indicates dbh) and the concentric red circles log-transformed epiphyte abundances on each tree (maximum 1692 individuals). The square indicates the location of the canopy crane. The plot covers two slopes alongside a small creek (c. 2 m wide) which is visible across the map (SW-NE). This figure only captures the horizontal part of the spatial distribution of epiphytes, but already documents a substantial heterogeneity in spatial distribution and the somewhat surprising finding that even many large trees may entirely lack epiphytes. It remains to be shown whether this is simply due to chance or whether factors such as host tree identity, topography, and small microenvironmental differences are causal.

(continued)

Box 7.2 (continued)



The vertical distribution adds complexity to this spatial structure. Species usually show a clear stratification, as illustrated for three bromeliad species. (For each species the proportions per 5 m height class are given.)



Some additional aspects of community structure, which have already been addressed in this community, are the relative abundance of functional groups (e.g., the prevalence of CAM), interspecific and intraspecific variation in other important traits (Petter et al. 2016), or the importance of regeneration in shaping the observed vertical patterns (Wagner et al. 2013).

(continued)

Box 7.2 (continued)

An important aspect of this work and the potential for the analysis of the collected data on epiphytes is the connection with the Center of Tropical Forest Science (http://www.forestgeo.si.edu). Information on the identity of all trees in the plot is available and all individuals are censused in regular intervals. This allows, e.g., age estimates of individual trees and the reconstruction of the establishment dynamics of epiphyte communities on individual tree species over many decades (e.g., Zotz and Vollrath 2003).

Work with tree assemblages has underlined the great value of a network of plots studied with comparable methodologies. The analysis of the resulting datasets allows much broader generalizations than single plot studies (e.g., Condit et al. 2005). In conclusion, we highly recommend the establishment of more plots to monitor vascular epiphytes with a long-term perspective. Substantial synergisms can be reached by establishing them, if possible, in already setup tree plots.

7.2.1 Vertical Structure

Forests are usually characterized by pronounced vertical environmental gradients, in particular in humidity and radiation (Sect. 5.1). In addition, other site characteristics such as the longevity of the substrate and its temporal availability for colonization (stem > branch > twig), bark rugosity, and water holding capacity are all likely to change with height above ground as well (Cabral et al. 2015), thus exacerbating the differences in water availability due to microclimatic gradients. This vertical gradient with associated differences in abiotic conditions should promote species sorting (sensu Chase and Leibold 2003). Together with typically low epiphyte densities, which lower the chance of competitive exclusion, this should allow the coexistence of a large number of ecologically equivalent species within each "vertical zone."

Indeed, a pronounced vertical stratification in the distribution of epiphytes is a very common observation (Pittendrigh 1948; Zotz and Vollrath 2003; Nieder et al. 2000), even in small-statured host trees like *Annona glabra* (Zotz 1997). This immediately suggests a direct causal connection between environmental gradient and epiphyte distributions. Almost a century ago, Van Oye (1924) proposed the first scheme to analyze epiphyte assemblages using distinct vertical zones on a given host tree. A number of additional schemes were proposed in subsequent decades, but the most commonly accepted was developed by Johansson (1974) for large host trees in West African rainforest. This scheme is not based on absolute height, but rather on the principal structures of the host tree (Fig. 7.11, e.g., lower portion of the trunk = zone I, basal part of larger branches = zone III, etc.). Attempts to align the five Johansson zones (JZs) with distinguishable epiphyte associations usually failed (e.g., Bøgh 1992; ter Steege and Cornelissen 1989;

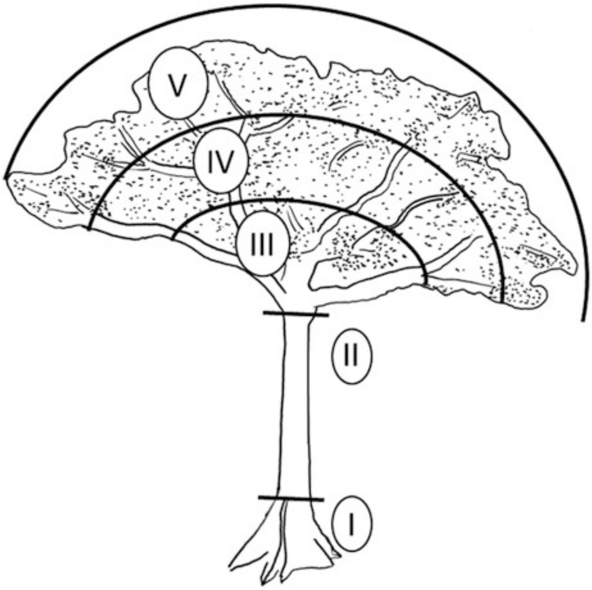


Fig. 7.11 Johansson-Zones. This zonation scheme, originally designed for large trees by Johansson (1974), has been frequently used in epiphyte research. The five zones are defined in relative terms along the trunk and within the tree crown. Although formally applicable to many other tree architectures, comparisons between studies are difficult and congruence with epiphyte associations is limited. In spite of these limitations, its continued use may still be recommended when additional data are collected, e.g., on the relative position of a focal tree in the vegetation, bark characteristics, etc

Ibisch 1996; Ek 1997; Nieder et al. 2000; Kelly et al. 2004). For example, Bøgh (1992) found no distinction between JZ IV and JZ V, and also combined JZ I and JZ II. Ek's (1997) agglomerative cluster analysis with the data of a floristic epiphyte survey in four lowland forests in the Guayanas showed no congruence with the Johansson zones either. More recently, Zotz (2007) used a comprehensive dataset of the epiphyte assemblage of 0.4 ha of pristine lowland forest in Panama to analyze its spatial structure without predefined zones. Included information for each of the 13,000 epiphytes was only height above ground, diameter and inclination of the substrate as continuous and tree stem as categorical variables. This analysis yielded six clusters, which more or less resembled JZs. However, one species cluster combined a group of epiphytes like *Dicranoglossum panamense* and *Peperomia rotundifolia* that preferentially grew on small diameter stems and branches of trees with small dbh (=diameter at breast height) at lower and intermediate heights within the forest. Johansson's tree-based approach would not have detected this ecological group, which comprised almost 10 % of all taxa. The results of another study indicate that this finding was not idiosyncratic to that particular site in montane forests in Bolivia, Krömer et al. (2007) identified a similarly distinct "understory zone," which represented an even larger proportion of the local epiphyte flora, i.e., 20 %. The important message of these two papers: although formally belonging to the same JZ, one should not lump the epiphytes found in the crowns of larger and smaller trees. In spite of all these limitations, researchers will probably not discontinue the use of Johansson´s scheme, simply for lack of a better alternative.

A number of generalizations are possible from the available reports of vertical structure in moist and wet forests. Taxonomically, the epiphyte flora of the outer canopy is dominated by orchids and bromeliads (in the Neotropics), while the lowermost stratum is mostly colonized by ferns, particularly typical are hygrophilous filmy ferns (Zotz and Büche 2000). There are also systematic differences in functional traits. Similar to the trends found in forests differing in precipitation, the proportion of species with CAM also changes along the vertical gradient within a forest. This has been shown for bromeliads in Trinidad by Griffiths and Smith (1983) and for two entire epiphyte assemblages in lowland Panama (Zotz and Ziegler 1997; Zotz 2004). A relatively little explored aspect is the phenotypic plasticity of individual species. A recent study, which assessed ten leaf traits (e.g., specific leaf area, $\delta^{13}C$, leaf thickness) of > 1000 individual epiphytes belonging to 83 species, found a positive correlation between intraspecific trait variability and the vertical range occupied in a number of species (Fig. 7.2, Petter et al. 2016).

7.2.2 Horizontal Structure

Different host tree species may offer a variety of microenvironments to vascular epiphytes, adding additional structure to epiphyte communities. Moreover, there are habitat specialists among epiphytes, which are almost exclusively found on particular substrates (e.g., many Catasetinae on dead wood), or in association with other canopy-dwelling organisms (e.g., ant-nest specialists such as *Peperomia macrostachya*, Sect. 8.3.5).

Epiphytes frequently show a highly clumped distribution (e.g., Nieder et al. 2000; Zotz and Schultz 2008) with some indications of taxonomic differences: orchids may be more clustered than other groups (Hietz and Hietz-Seifert 1995). Such a pattern could reflect the varying suitability of particular host tree species or substantial dispersal limitation. As a corollary, the majority of trees in lowland forest are usually free of epiphytes. For example, at a site in lowland Panama fewer than 30 % of 1400 inspected, seemingly inhabitable, trees (dbh > 1 cm) hosted at least one epiphyte (Zotz and Schultz 2008). A similarly high proportion of "empty" trees has been reported from diverse lowland sites in Asia, Africa and the Americas (Table 7.1). Montane sites are clearly different, although the database is much scarcer. Noteworthy, however, even at montane sites it is not unusual to find a certain percentage of trees without epiphytes. For example, while all inspected 105 trees with a dbh > 5 cm in a lower montane rainforest in Panama were host to lichens and mosses, a fourth of them were devoid of vascular epiphytes (D. Gómez, unpubl. results). Why are so many trees in lowland forests free of epiphytes, even in wet forests? One part of the answer is the fact that some tree species are poor hosts

Table 7.1 Proportion of trees with epiphytes in different tropical lowland and montane forests

Location	Elevation	# of trees	Minimum size	% with epiphytes	Source
Moraballi Creek, Guyana	Lowland	193	>5 m height	16	Davis and Richards (1933, 1934)
Moraballi Creek, Guyana	Lowland	55	>14 m height	38	Davis and Richards (1933, 1934)
Shinguipino, Ecuador	Lowland	42	>6 m height	60	Grubb et al. (1963)
BCI, Panama	Lowland	1210	c. 6 m	50	Zotz et al. (1999)
Surumoni, Venezuela	Lowland	1085	>10 cm dbh	13	Nieder et al. (2000)
Amazonia, Colombia	Lowland	1701	>2.5 cm dbh	40–60	Benavides et al. (2005)
Amazonia, Colombia	Lowland	c. 1000	>5 cm dbh	50–85	Benavides et al. (2005)
San Lorenzo, Panama	Lowland	1373	>1 cm dbh	28	Zotz and Schultz (2008)
Shasha Reserve, Nigeria	Lowland	142	>5 m height	15–24	Richards (1939)
Kidatu, Tanzania	Lowland	20	>5 m height	60	Johansson (1974)
Gunung Dulit, Sarawak	Lowland	135	>8 m height	12	Richards (1996)
Xishuangbanna, China	Montane	6 x 16	>10 cm dbh	56–100	Zhao et al. (2015)
Fortuna, Panama	Montane	105	>5 cm dbh	74	Gómez, Diana unpubl. data
Shinguipino, Ecuador	Montane	52	>6 m height	96	Grubb et al. (1963)

Also given are details on study site, the number and the minimum size of censused trees, and original sources

(e.g., with very smooth or shedding bark) and even as large individuals are not suitable for most epiphytes (e.g., *Jacaranda copaia* in lowland Panama, Zotz and Schultz 2008, Box 7.2); the major reason, however, is probably the very slow colonization of any tree by epiphytes (Fig. 7.12, Zotz and Vollrath 2003; Taylor and Burns 2015; Flores-Palacios and García-Franco 2006). Whether this is due to a relatively low number of diaspores, dispersal limitation, or establishment problems is not really resolved (Cascante-Marín et al. 2006, 2009). Large trees, which were available for colonization for many decades, usually host a disproportionate part of all locally occurring epiphytes. A few numbers shall illustrate the magnitude of this bias: 15 % of all epiphytes found in 0.4 ha of lowland forest in Panama were found on a single large *Brosimum utile* tree (Zotz and Schultz 2008) and 40 % of all epiphytes in a 600 m^2 plot in lowland Ecuador were found on just 3 trees (Grubb et al. 1963). Such a concentration of epiphyte abundance (and diversity) on large trees has important conservation implications (Kartzinel et al. 2013), particularly in

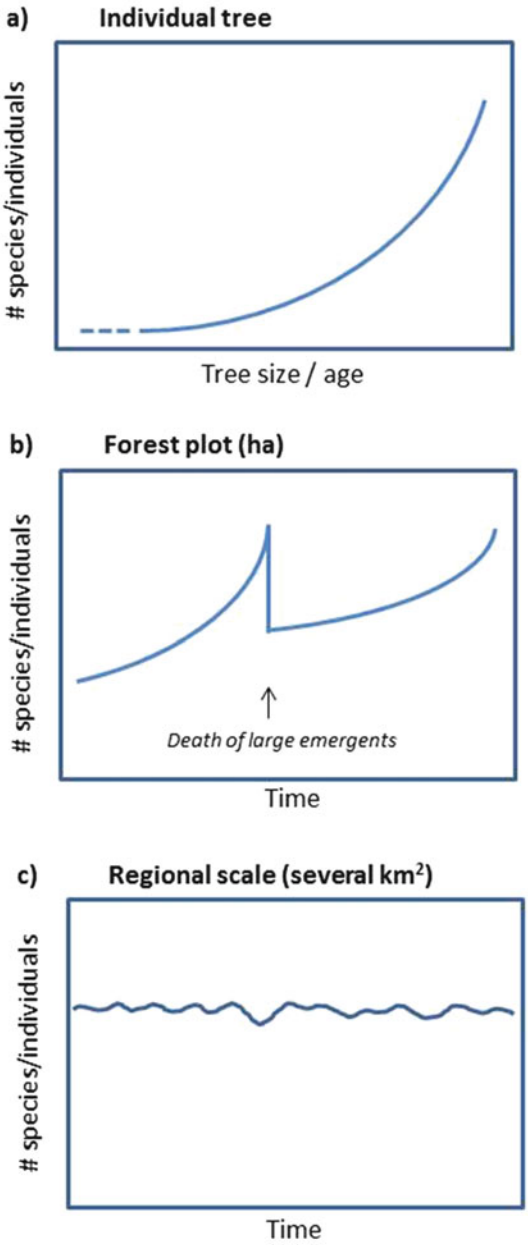


Fig. 7.12 Model dynamics of epiphyte assemblages at different spatial and temporal scales. The absolute species/individual numbers and the time axis will differ depending on (**a**) tree size and suitability of a given host tree species; (**b**) the regional species pool; (**c**) the regional species pool

view of the fact that large, and old, trees are declining globally (Lindenmayer et al. 2012, Chap. 10).

Substantial dispersal limitation should also lead to spatial structure, i.e., a larger similarity of the epiphyte assemblages on neighboring trees than expected by chance. The results of the few studies that explicitly addressed this question do not yield a simple picture, which probably reflects different methodologies, spatial scales, taxonomic groups of epiphytes studied, and vegetation types. Statistical analyses revealed nonrandom spatial structure *within* a plot in a lowland forest (Zotz and Schultz 2008), but not *between* plots in Colombian Amazonia (Benavides et al. 2011), in contrast to, e.g., a study in pine-oak forests in Mexico (Wolf 2005). However, the fact that the similarity of epiphyte communities of these pine-oak forest plots was related to geographical distance was at least in part a consequence of an environmental gradient and not related to distance as such. A study in seven other oak forests in Mexico and Colombia (Wolf et al. 2009) failed to detect a correlation of distance between host trees and epiphyte community composition in all but one case. The results of population genetic studies of orchids in Costa Rica are also relevant in this context (Trapnell et al. 2004, 2013). These authors found significant, positive genetic structure in the orchid *Laelia rubescens* only at very small distances (Trapnell et al. 2004). A later study with *Brassavola nodosa* reached similar conclusions—significant relatedness was primarily found among individuals *within* a tree, which suggests that few colonization events of a tree are followed by a subsequent local population expansion (Trapnell et al. 2013). This scenario is in line with the conclusion of Zotz et al. (1999) who analyzed the spatial structure of epiphytes on hundreds of *Annona glabra* trees at two hierarchical levels, neighboring branches of a tree and among trees. They found high species presence/absence similarities among branches as compared to low presence/absence similarities among trees, which suggests that effective dispersal does not *gradually* decline with distance from the seed source, but mostly happens on a very local scale.

Spatial structure may also be related to local environmental gradients. For example, changes in epiphyte abundance with distance from water courses and other water bodies have frequently been observed. Unsurprisingly, e.g., trees growing close to a water-filled sinkhole ("cenote") in a dry forest in Yucatán, Mexico, have much higher densities of epiphytic bromeliads than more distant ones, a pattern arguably related to higher nighttime humidity near these water bodies (Chilpa-Galván et al. 2013). Less expectedly, there are reports that indicate that such an effect of water courses on epiphytes is not restricted to dry environments. Even in wet lower montane rainforests, epiphyte densities may show steep declines as one moves away from water courses (e.g., Richardson 1999; Flores-Palacios and García-Franco 2008).

7.3 Community Dynamics

Since epiphytes grow on a living substrate, they are subject to dynamics imposed by the host tree, in addition to the endogenous dynamics of the epiphyte population. This exogenously imposed dynamic is strongly scale dependent, from the fatal effect of the flaking of a small piece of bark on one tiny seedling to the demise of thousands of large epiphytes when a large emergent tree falls. An already established individual will also experience changes in microclimate over time as, e.g., a particular site may be overgrown and shaded by the expanding crown. Ultimately, the potential life expectancy of an epiphyte is determined by the longevity of the substrate. Once fallen to the ground, whether with or without substrate, chances of survival are generally rather limited (Sect. 6.5). On the other hand, as a tree grows, new opportunities for the establishment of new recruits are continuously produced (Fig. 7.12). A growing tree does not only produce *more* opportunities, but also *qualitatively* different ones, which has already been pointed out by Johansson (1974). For example, a tree sapling growing in the understory will not be host to heliophile species, but as it grows larger and becomes an emergent tree, this situation changes (Zotz and Vollrath 2003). Since early arrivals are usually not replaced by individuals that establish later on, there is a continuous increase in species numbers and abundance with time on any given tree (Flores-Palacios and García-Franco 2006). As long as no major tree falls occur, this increase in epiphyte species richness and abundance on individual trees scales up to a local forest stand. Indeed, in all cases with repeated censuses, there were (substantial) increases (Schmit-Neuerburg 2002; Laube and Zotz 2006a, 2007) without signs of saturation. For example, within four years, the number of epiphytes in 1 ha of lowland forest in Venezuela increased from 940 individuals (55 species) to 1516 individuals (71 species) (Schmit-Neuerburg 2002). Similarly, in 0.4 ha of lowland forest in Panama, the number of individual epiphytes rose from c. 11500 individuals (104 species) to >17,000 individuals (110 species) in 10 years (G. Mendieta-Leiva and G. Zotz, unpublished data). Both were mature forests without major anthropogenic or natural disturbance. Hence, both a larger, regional sampling and a longer time interval between censuses on that local scale would arguably document a steady-state situation (Fig. 7.12). This is probably different in natural forests with frequent and massive disturbances such as forests in the Caribbean with regular Hurricane impacts (Sect. 7.3.2), but I am not aware of any published evidence to test this notion.

7.3.1 Succession

A tree sapling starts growing without epiphytes. Hence, epiphyte assemblages on a given tree will always have started “from scratch.” Dudgeon (1923) has introduced the concept of “succession” among epiphytes into the literature. Unfortunately, this term is frequently used rather loosely: if succession only signifies a change in the species structure of an ecological community over time, the existence of succession among epiphytes is obviously a truism and the use of this term thus rather meaningless. If, however, succession is more narrowly and arguably more properly defined as the biological process, in which directional and predictable changes in species composition and abundance are brought about by changes in the substrate or by colonizing pioneer epiphytes, with immigration and extinction of species (Crawley 1997), the question of the occurrence and possible importance of succession among epiphytes demands more attention.

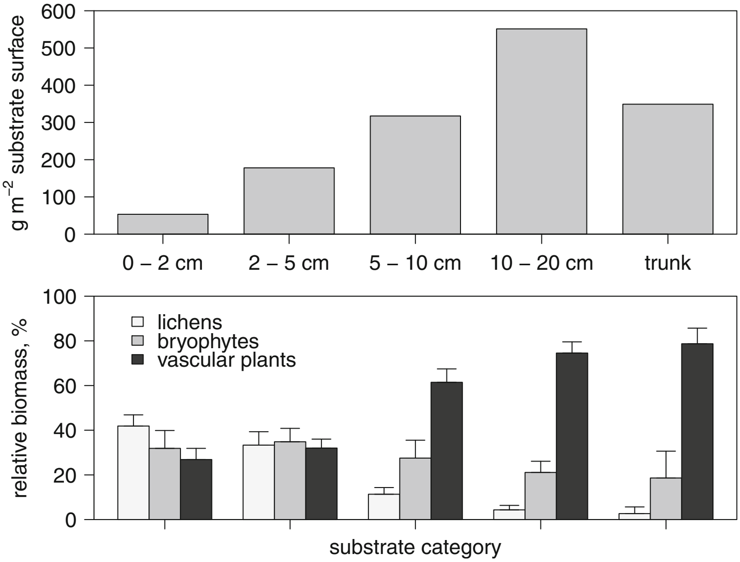


Fig. 7.13 Successional changes in different groups of epiphytic organisms within tree crowns. Total epiphytic biomass (*upper plot*) and contribution of different biomass components (macrolichens, bryophytes and vascular epiphytes (ferns and angiosperms) to total epiphytic biomass (*lower plot*) in a lower montane forest in Ecuador on branches of different diameters and trunks (disregarding diameter). Data are means (± SD) of three adjacent forest types. Data are from Werner et al. (2012)

In systems without substantial accumulation of dead organic material (= DOM, e.g., in moderately moist or dry lowland forest), species that appear first are usually not replaced over time; established individuals persist and local recruitment continues (Benavides et al. 2006; Zotz et al. 1999; Wallace 1981). Changes in species composition merely due to later arrival of additional species are clearly not related to a successional process, but result in a steady accumulation of species with tree age—most published studies suggest such a trend (reviewed in Flores-Palacios and García-Franco 2006). Particularly in systems with a substantial accumulation of DOM, however, the previous colonization with bryophytes and lichens and more drought-tolerant vascular species may constitute an obligatory step that facilitates the establishment of less drought-resistant species, while pioneers may be replaced in turn. For example, in temperate rainforests of New Zealand, shrubby *Brachyglottis kirkii* is usually found growing in nest epiphytes such as *Astelia solandri* or *Collospermum hastatum* (Kirby 2014) and arguably depends on their previous establishment. Still, conceptually, this may rather be interpreted as a facilitation cascade (Thomsen et al. 2010) and not as a true succession. "Nest-epiphyte communities" in some Australian forests are another well-documented example of similar nature described in detail by Wallace (1981). A typical sequence starts with the establishment of a fern (a species of *Drynaria* or *Platycerium*) on bare bark. With increased size and accumulation of organic material around their fronds, these nest ferns provide suitable substrate for the germination of hemiepiphytic *Ficus*, other epiphytic ferns, and vascular epiphytes like *Hoya* sp. or *Cymbidium* sp. Species assemblages are richest when the fern itself already starts to decline. Interestingly, final dislodgement of the nest-former usually also results in the end of the “invaders”—they apparently depend on the habitat modifications of the nest fern for survival and not only for establishment. Both examples, which report side-by-side observations, fall short of demonstrating actual species replacement among co-occurring vascular plants, but other studies provide at least indirect evidence for such a process among nonvascular and vascular epiphytes. For example, Werner et al. (2012) interpret their data of epiphytic matter (Fig. 7.13) along a twig–branch–trunk trajectory in a montane forest in Ecuador as evidence for the replacement of lichens by bryophytes and vascular epiphytes. However, the *relative* reduction in the contribution of lichens to total biomass by one order of magnitude is mostly the result of a massive increase in the biomass of mosses and angiosperms and less due to an *absolute* decline of lichens by possible replacement.

In summary, the importance of successional processes for the community dynamics of vascular epiphytes is an open question. Most examples described above can be more appropriately described as facilitation cascades. Even in situations in which true succession may occur, both temporal trajectories and ecological importance are largely unresolved. It should be possible to provide unequivocal documentation of such replacements, e.g., by repeated photographs (compare Hietz 1997 for the application of photographs in a demographic study). Although such a study would not be suitable for a typical PhD thesis, it certainly is within the scope of tenured researchers—Werner and Gradstein (2008) report that after experimental removal epiphytes start to accumulate within 2–3 years on tree trunks in a montane setting in Ecuador, while in a similar experiment in a montane forest in Mexico epiphyte densities of colonizer communities were already indistinguishable from those of established community after five years (Acuña-Tarazona et al. 2015).

7.3.2 Disturbance

Disturbance comes at different scales, frequencies, and intensities (Crawley 1997). Some major agents of disturbance for soil-rooted plants, e.g., landslides, will affect epiphytes only indirectly via its effect on the host tree, others such as fire may be primarily relevant for trunk epiphytes in some savannas (Fig. 7.9c, Adams and Lawson 1984), and yet others, e.g., storms, can impose a similar, direct impact on both epiphyte and host. Of particular and distinctive importance for epiphytes is disturbance that is caused by the host itself. This type of disturbance may concern just parts of an individual, e.g., when a single root is dislodged, or a subset of the local epiphyte community, e.g., when flaking of small portions of bark only affects juveniles, which fall off as entire individuals. On the other hand, branch fall, let alone tree fall, should affect epiphytes irrespective of plant size (Cabral et al. 2015). The propensity of individuals to be dislodged during extreme storms is a function of their location within a crown (Batke and Kelly 2015; Oberbauer et al. 1996); whether plant size and species identity also plays a role is unclear, but seems likely. Mortality after a tree fall, on the other hand, is probably independent of plant size. A final agent of disturbance merits mention: arboreal animals. Monkeys sometimes remove larger epiphytes from major limbs when obstructing their major foraging routes (Perry 1978); others, e.g., kinkajous, have communal potties that squash plants (Cardelús, pers. obs.). To date, the treatment of this issue is clearly at an anecdotal stage and the overall impact on epiphyte communities remains unclear. Unless animal action is directly observed, the frequent absence of epiphytes from the upper part of large limbs (Fig. 7.9d) may also be explained by challenging water relations.

There is very little quantitative information on the importance of these agents of disturbance for community dynamics. Good quantitative evidence is available for the local effect of "substrate instability" on epiphyte populations (e.g., Hietz 1997; Zotz et al. 2005). Generally speaking, branch and tree falls seem to be the principal, sometimes only, causes of mortality of larger individuals, while smaller conspecifics die for a number of reasons, frequently because of desiccation (Table 6.2).

In contrast to the available quantitative evidence on the importance of substrate instability for epiphyte population dynamics, information on the impact of severe storms on epiphyte community structure and dynamics is mostly anecdotal. There are at least 20 reports on storm impact, mostly focusing on hurricanes, but also on the effect of unspecified "storms" (Table 7.2). These studies document anything from marginal to substantial damage to the resident epiphytes (e.g., >90 % mortality, Loope et al. 1994). Unfortunately, the presented data hardly allow generalizations. First, although some at least mention top wind speeds, the actual forces in the focal area are not specified, which makes it difficult to compare studies. Moreover, there is no information in the literature on the drag that epiphytes can actually sustain: the minimal wind speed capable of dislodging a plant has not been determined for any epiphyte. Hence it is unclear which wind speed can actually be considered "critical." Second, the temporal scope is mostly very limited. With these limitations in mind, what can we learn from a review of the studies compiled in Table 7.2? Not surprisingly, the short-term effect is invariably negative with high mortality, but long-term effects are much more varied. For example, there are indications of very fast recovery that even overcompensates losses (Oberbauer et al. 1996). Some studies report substantial change in community composition after storms (e.g., Lowman and Linneroth 1995), others none (e.g., Goode and Allen 2008).

There are some recent advances, such as the application of population viability analysis to quantify the impact of hurricane frequency on population growth of an epiphytic orchid (Raventós et al. 2015b) or landscape level assessments of the impact of hurricanes on epiphytes and other structurally dependent plants (Batke and Kelly 2015). Overall, however, we are still largely ignorant of the long-term

Table 7.2 Studies on the impact of hurricanes and other storms on vascular epiphytes

Geographical region	Event	Aspect	Method	Taxa	Source
Cuba	Hurricane Ivan	Demography after disturbance	Matrix analysis post-hurricane	2 orchid species	Mújica et al. (2013)
Cuba	Hurricane Ivan	Transient population dynamics	Modeling	2 orchid species	Raventós et al. (2015a)
Cuba	Hurricane Ivan	Viability analysis	Field observation	1 orchid species	Raventós et al. (2015b)
Cuba	Hurricane Ivan	Recovery	Field observation	2 orchid species	Wiegand et al (2013)
Cuba	Several hurricanes	Demography	Field observation	1 orchid species	Vale et al. (2013)
Florida	"no-name storm"	Mortality after storm	Field observation	4 species	Lowman and Linneroth (1995)
Florida	Hurricane Andrew	Immediate damage	Field observation	Many species	Loope et al (. 1994)
Florida	Hurricane Andrew	Damage and recovery	Inventories pre- and post-hurricane	5 bromeliad species	Oberbauer et al. (1996)
Florida	Hurricane Andrew	Recovery	Field observation	4 bromeliad species	Robertson and Platt (2001)
Florida	Hurricane Donna	Immediate damage	Quantification of damage	Many species	Craighead and Gilbert (1962)
Guam	Typhoon Paka	Impact of epiphytes on host tree	Field observation	Epiphytic ferns	Marler and Lawrence (2013)
Honduras	Several hurricanes	Impact on all dependent plants	Field observation	Many species	Batke and Kelly (2015)
Japan	Storm	Demography after disturbance	Matrix analysis post hurricane	1 orchid species	Matsumura and Sawada (2009)
Mexico	Hurrican Wilma	Immediate damage	Field observation	Many species	Goode and Allen (2008)

Puerto Rico	Hurricane George	Demography after transplantation	Matrix analysis post-hurricane	1 orchid species	Benítez-Joubert and Tremblay (2003)
Puerto Rico	Hurricane George	Survival after relocation	Field observation	1 orchid species	Tremblay (2008)
Puerto Rico	Hurricane Hugo	Impact of epiphytes on host tree	Field observation	n/a	Frangi and Lugo (1991)
Puerto Rico	Hurricane Hugo	Immediate damage	Field observation	11 orchid species	Migenis and Ackerman (1993)
Puerto Rico	Hurricane Hugo	Immediate damage	Field observation	1 orchid species	Rodríguez-Robles et al. (1990)
Puerto Rico	Hurricane Hugo	Damage and recovery	Field observation	Many species	Weaver (1999)
Puerto Rico	Unspecified	Survival after dislodgement	Experimental transplantation	1 bromeliad species	Pett-Ridge and Silver (2002)

Given are details on study site, storm event, the studied aspect of epiphyte performance, method, included taxa and the original publication effects of tropical storms on epiphyte communities, beyond the general statement that “strong winds” cause, at least, short-term damage. If the incidence of tropical storms increases in the future as predicted (Goode and Allen 2008), it is vital to understand which disturbance frequency and intensity will still provide sufficient time for the recovery of epiphyte communities. Currently, we are not capable of making any informed predictions.

Finally, there is an additional aspect of the impact of strong winds that has been mentioned in a few studies (e.g., Marler and Lawrence 2013): the presence of epiphytes may negatively affect the stability of the host tree. Epiphytes increase the resistance to wind, thus promoting the likelihood of stem breakage during a hurricane (e.g., Frangi and Lugo 1991). As in many other cases described in this monograph, however, it is unclear whether these observations are of general relevance.

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Interactions with Other Organisms

8

8.1 Interactions with the Host Tree

By definition, epiphytes are structurally dependent on their hosts, and the notion of host specificity is as old as the scientific study of vascular epiphytes (Schimper 1888). The relevance of host tree identity for the composition of epiphyte assemblages, which has been touched in over 200 papers in one way or another (Wagner et al. 2015), has been discussed in detail in Sect. 7.2.

While host tree identity most likely impacts the establishment, growth and survival of epiphytes, these may in turn affect their host tree as well. A negative impact of structurally dependent plants on the host tree has sometimes been treated as parasitism (e.g., "structural parasitism," Montaña et al. 1997; Stevens 1987), but the use of the term "parasite" seems inappropriate since a connection to live tissue of the host is missing (Moffett 2000). Competition is not a satisfying term either for all the facets of the negative impacts of epiphytes on hosts, and it has been become customary to use the term "piracy." This can be either "nutritional piracy" (Benzing and Seemann 1978) when minerals are intercepted, thus reducing nutrient flow to the root zone of the tree, or "structural piracy" when epiphytes weigh down or physically impede the growth of their host. It has been proposed that heavy loads of epiphytes and lianas in some forests even increase host tree dynamics by causing higher rates of tree falls (Strong 1977), partly because heavy epiphyte loads increase wind drag (Marler and Lawrence 2013). There is the plausible but untested hypothesis that differences in the bark structure or dynamics of potential hosts (e.g., flaking bark) or the presence of spines in palms are partly related to the avoidance of epiphytes (Montaña et al. 1997; Benzing 1990; Maier 1982). Similarly, Page and Brownsey (1986) interpret the retention of old fronds as fringing "skirts" around the trunks of some tree ferns and palms as a protection against climbing plants and large epiphytes. Although not unreasonable, this notion has hardly been studied properly. Montaña et al. (1997) report a negative correlation of epiphyte load and the percentage of life shoots on *Cercidium praecox* trees in dry scrub in Mexico, but offer no mechanistic explanation for their observation. Finally, experimental

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removal of *Tillandsias* stimulated leaf production in *Prosopis* trees (Soria et al. 2014). Taken together, there is suggestive evidence that the relationship of epiphyte and host is not always entirely commensalistic, but generalizations about occurrence and intensity of nutritional or structural piracy would still be premature. Competition for light between epiphytes and host tree foliage has also been invoked (Benzing 2012). However, while there is no doubt that other structurally dependent plants such as stranglers and lianas can be severe competitors for light (Lüttge 2008; Putz and Holbrook 1986), any substantial impact of epiphyte shading on tree carbon balance is probably limited to exceptional cases.

There is the long-standing yet still unsubstantiated claim that epiphytic growth may lead to a deterioration of tree vigor by other mechanisms than those discussed above. Ruinen (1953) called this imaginary or real phenomenon "epiphytosis." She argued that the fungal partner of epiphytic orchids could become virulent and harm the host, but the provided evidence was ambiguous. Others detected differences in bark tissue with and without epiphytic bromeliads, proposing a higher susceptibility to pathogen attack unrelated to mycorrhizae in epiphytic bromeliads (e.g., Aguilar-Rodríguez et al. 2007). Few studies go beyond a descriptive approach, which cannot distinguish cause and effect in the association of reduced tree vigor and epiphyte abundance, and none provides really convincing evidence that epiphytosis is ecologically important. It seems unlikely that allelochemicals of epiphytes such as the atmospheric bromeliad *Tillandsia recurvata*, which can negatively affect host trees in desert scrublands (Flores-Palacios et al. 2014), are relevant in other more species-rich moist forests.

Similarly unclear is the ecological importance of adventitious tree roots, which have been originally described by Herbert (1958) and later studied in more detail by Nadkarni (1981). If these roots, which can form extensive networks beneath epiphyte mats in some temperate and tropical rainforests, are indeed functionally important, there are two major consequences: (1) since the N cycle of canopy soil/epiphytes seems to be largely independent from the host tree–ground soil N cycle (Hietz et al. 2002), adventitious tree roots may connect these two cycles, and (2) adventitious roots will allow trees to directly compete with epiphytes for nutrient resources in the canopy. Support for this scenario is mixed. Hertel and Köhler (2010) compared fine root biomass of oak trees in the canopy and the terrestrial organic layer in a montane forest in Costa Rica with particularly nutrient-poor soils and found that canopy fine roots accounted for a mere 0.04 % of that in the terrestrial layer. Moreover, canopy roots completely lacked ectomycorrhizae, while terrestrial fine roots were heavily colonized. Consequently, Hertel and Köhler (2010) concluded that the nutritional benefit from canopy roots for the host tree must be marginal. However, adventitious roots of *Nothofagus* trees in New Zealand had abundant mycorrhizal fungi (Orlovich et al. 2013), and these authors suggested functional significance for both hosts and epiphytes. However, relatively high concentrations of nutrients in some canopy soils are not indicative of large pools, which should be much higher in the soil. Moreover, one should bear in mind that in many or even most tree canopies large accumulations of organic material are lacking or are largely confined to the inner crown on thick, horizontal branches.

There are scattered reports on other indirect effects that epiphytes may have on their host tree. For example, the ant species *Crematogaster difformis* inhabits a number of myrmecophytic epiphytes of the genera *Lecanopteris* and *Platycerium* in tropical lowland rainforest in Borneo. Tanaka et al. (2009) showed that *Crematogaster difformis* not only regulates herbivorous insects potentially attacking their epiphytic hosts but also those that could feed on leaves of the host trees. Dejean et al. (1995) report a similar case of indirect protection of the host tree from low inundated forest in Yucatán: trees without epiphytes were heavily attacked by leaf-cutter ants, while trees with epiphytes inhabited by ants were left intact.

In conclusion, to date the nature of the impact of epiphytes on their host tree (and vice versa) is not entirely understood, although in general a more or less communalistic relationship seems to be the most probable. Future studies should try to achieve a quantitative evaluation of the relative importance of these biotic interactions for different vegetation types, with the long-term goal of a general understanding of the intricacies of the epiphyte–host relationship.

8.2 Interactions Among Epiphytes and With Other Structurally Dependent Plants

The individual epiphyte shares its habitat with many other structurally dependent organisms. First of all, an epiphyte may interact with other vascular epiphytes. Ecological theory predicts that plants in physically stressful environments should show more positive than negative interactions (Bertness and Callaway 1994), but reports of both, positive interactions (e.g., facilitation) and negative ones (e.g., competition), are quite rare. This may represent a lack of research or, alternatively, reflect that biotic interactions among vascular epiphytes are indeed not very important in shaping epiphyte assemblages because densities are frequently very low. Densities are rarely quantified, but the figure of c. 1 epiphyte m^{-2} bark surface on *Socratea exorrhiza* reported by Zotz and Vollrath (2003) is probably not unusual for many lowland forests. This situation would be comparable to understory shrubs in tropical forests where abiotic conditions also result in low densities and plants thus rarely interact with one another (Wright 2002).

One of the few documented examples of facilitation stem from a subtropical rainforest in China, where a co-occurring fern enhances water availability to *Haplopteris zosterifolia* (Jian et al. 2013), and another from temperate forests in New Zealand: humus-accumulating *Collospermum* and *Astelia* nest epiphytes provide a safe site for germinating shrub epiphytes (Dawson 1988, see also Sect. 7.3.1). Facilitation may also be more indirect. For example, it seems well established for terrestrial orchids that germinating seeds benefit from the spatial proximity to a larger conspecific because of the provision of the essential mycorrhizal partner among (Rasmussen et al. 2015), but it has rarely been evaluated whether this is also the case among epiphytic taxa. A study with *Epidendrum firmum* found no such effect (Kartzinel et al. 2013). Overall, it remains unclear how important such facilitative processes are for orchids and for epiphytes in general.

The same is true for the competition, for which information is similarly anecdotal. For example, during a demographic study with the heteroblastic bromeliad, *Vriesea sanguinolenta*, Zotz et al. (2005) observed that growth in the rain shadow of larger plants frequently led to the death of smaller conspecifics. Without a quantitative analysis, however, this finding can hardly be used to gauge its importance for the demography of this and other species or community structure at large. Potential allelopathic interactions among epiphytes have recently been studied by Valencia-Diaz et al. (2012): leachates and organic extracts of *Tillandsia recurvata* inhibited the germination of many other, co-occurring *Tillandsia* species. However, rates of inhibition seem to be unrelated to spatial association patterns, which argues against an important role of allelopathy in community assembly.

Vascular epiphytes share their habitat with other groups of autotrophs, which sets the scene for possible interactions with, e.g., nonvascular epiphytes (algae, mosses, liverworts, and lichens), lianas, hemiepiphytes, and hemiparasitic mistletoes. Many reports propose that the presence of epiphytic bryophytes facilitates the establishment and survival of vascular epiphytes (Sect. 7.3, e.g., Van Leerdam et al. 1990; Tremblay et al. 1998; Zotz and Vollrath 2003). Bryophytes may affect epiphyte establishment by improving anchorage for seeds and by causing a more reliable water supply during germination, particularly in tree species with smooth bark (Wyse and Burns 2011), but also by reducing the severity of drought in later ontogenetic stages—this effect is expected to be a decreasing function of plant size (Zotz et al. 2001). Finally, higher humidity in bryophytes may also promote the formation of orchid mycorrhizae (Osorio-Gil et al. 2008).

The association of vascular epiphyte and bryophytes can be very tight in some cases. For example, the epiphytic fern, *Polypodium glycyrrhiza*, was exclusively found in moss mats with thick layers of underlying humus in Douglas fir forest in Oregon (Sillett 1995). A similarly tight spatial association of epiphytic *Polypodium vulgare* with moss was observed in a montane forest in the Swiss Alps (Zotz 2002). Although bryophyte mats covered only about 10 % of the available tree bark, *Polypodium vulgare* was exclusively found in thick moss. In many cases, however, moss may just be a facilitator rather than an essential requirement for successful establishment of vascular epiphytes (Chap. 7). In a study of the epiphytes on *Socratea exorrhiza*, a palm with smooth bark, epiphytes were more frequently found in patches of bryophytes than expected by chance, but a majority of individuals had obviously been able to establish on naked bark or on crustose lichens (Zotz and Vollrath 2003).

Such one-time observations cannot provide strong evidence for causality, and neither can repeated observations such as those by Scheffknecht et al. (2010), who demonstrated a negative correlation of mortality in epiphytic *Lycaste aromatica* and the bryophyte cover on supporting branches. Experimental approaches are necessary to resolve the issue, but there are only three relevant studies (Cascante-Marín et al. 2008; Laman 1995; Nadkarni and Solano 2002). Laman (1995) focused

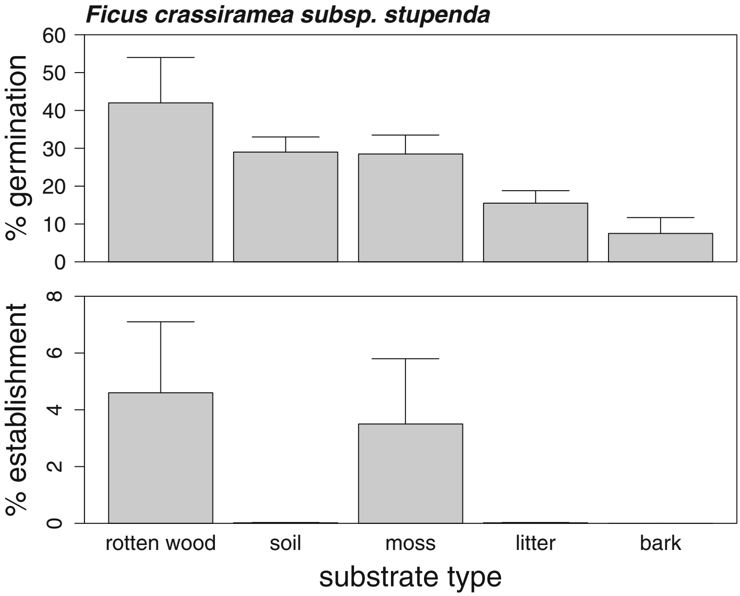


Fig. 8.1 Germination success (*upper panel*) and establishment of seedlings (*lower panel*) of *F. crassiramea* ssp. *stupenda* in natural canopy sites in relation to substrate types. Values are means ± SE of 7–12 replicates (germination) and 22–100 replicates (establishment). Establishment was assessed 12 months after planting. Modified after Laman (1995)

on germination and seedling establishment of hemiepiphytic *Ficus crassiramea* subsp. *stupenda* in Borneo. Germination success on substrates with good moisture retention (moss or rotting wood) was 3–4 times higher than on pure bark (Fig. 8.1). Although bare soil was also a good substrate for *Ficus* seeds to germinate, subsequent survival was as low as on bark or on litter. The effect of bryophytes on germination of four bromeliad species in Cascante-Marín et al. (2008) study was less impressive: the presence of bryophytes led to an increase in germination of ca. 30 %. Finally, Nadkarni and Solano (2002) report an enigmatic finding. They transplanted entire portions of branches with epiphytes and arboreal soil from upper cloud forest to slightly lower elevations and detected a suppressed "terrestrial" seed bank in these mats. To conclude, the studies of Laman (1995) and Cascante-Marín et al. (2008) provide rare examples of unambiguous evidence for an important, positive effect of the presence of moss on the establishment of vascular epiphytes. Studies with similar results from, e.g., bare limestone habitats with comparable ecology (Sand-Jensen and Hammer 2012), suggest larger applicability of these findings.

However, there are also a few contrasting observations with nonvascular epiphytes. For example, Winkler et al. (2005a) observed not only positive (e.g., in *Tillandsia deppeana*) but also at least one negative correlation (in *Tillandsia multicaulis*) of plant survival and bryophyte cover in a montane forest in Mexico. In addition, I repeatedly observed that foliose lichens overgrew and presumably killed slow-growing seedlings of epiphytic orchids, both in lowland forests and in montane forests (Zotz and Schleicher 2003; Zotz et al. 2014).

Possible interactions of epiphytes with other co-occurring canopy plants, e.g., lianas, hemiepiphytes, or mistletoes, have rarely been studied. For example, I am not aware of a single study that would have contrasted the suitability of lianas vs. trees as hosts for epiphytes. At least one study addressed germination on hemiepiphytes (Titus et al. 1990). However, that study focused exclusively on the aspect of autotoxicity among strangler figs. There are a few anecdotal reports that baskets of epiphytic *Drynaria* and *Asplenium* ferns are sometimes used as establishment sites for strangler figs (Schmidt and Tracey 2006), similar to the observation that *Clusia rosea* may establish in bromeliad tanks (Lüttge 2008). Without more rigorous assessments, such observations provide limited insight into possible ecological importance. There is circumstantial evidence that abundant lianas may suppress epiphyte establishment. Comparing secondary and old-growth forests in the Dominican Republic, Martin et al. (2004) found very few epiphytes in secondary habitats and speculated that unusually abundant vines had suppressed epiphytes by increasing shade and occupying colonization sites. A similar observation was made by Magrach et al. (2014).

8.3 Interactions with Animals

Tropical forests are known to be the most species-rich terrestrial ecosystems and much of this diversity is found in the canopy. Thus, there is a rich potential for species interactions of epiphytes with co-occurring fauna, in particular arthropods. These interactions bridge the entire range from positive (e.g., pollination and dispersal) to neutral and negative (e.g., herbivory). Others are more diffuse or indirect, e.g., via habitat cascades (Thomsen et al. 2010). Similar to our current understanding of the relationship of epiphytes and host trees, most of these interactions are probably not very specific at the species level. However, there are a considerable number of examples for specializations, e.g., funariid birds which forage almost exclusively on epiphytic bromeliads (Sillett et al. 1997), numerous frogs (Fig. 8.2, Picado 1913; Wells 2007; McCracken and Forstner 2014), protists (Foissner 2010), and arthropods such as hydrophilid beetles (Clarkson et al. 2014), which seem to depend intimately on phytotelmata. All of these types of interactions will be discussed in depth in this section.

8.3.1 Herbivory

Ecological theory predicts that resource-poor habitats should have a high proportion of species with long-lived and well-defended leaves (Coley et al. 1985). Since the epiphytic habitat is generally resource poor (Chap. 5), low levels of herbivory could be expected. Indeed, in a community level study in a humid montane forest in Mexico (Winkler et al. 2005b), the average annual leaf area loss in bromeliads and

Fig. 8.2 A considerable number of amphibians can be found in tank bromeliads in tree crowns, but dependence on these microlimnetic systems varies. Some of these arboreal anurans like *Pristimantis waoranii* (**a**) and *P. aureolineatus* (**b**) may depend entirely on bromeliads as refugia for life in the canopy. The poison arrow frogs *Ranitomeya variabilis* and *R. ventrimaculatus* (**c**) are more flexible, although bromeliads are preferred breeding sites. Yet others like *Osteocephalus fuscifacies* (**d**) are less selective (Shawn McCracken, pers. comm.). (Photographs (**a**)–(**d**): Bejat McCracken)

orchids was less than 1.5 % a^{-1}. This loss is considerably lower than average annual rates of leaf damage in other plant groups. In a review, Coley and Barone (1996) report rates of leaf area loss of 11 % a^{-1} and 48 % a^{-1}, respectively, for shade-tolerant tree species and gap specialists in tropical wet forests and 14 % $a^{-1}$for tropical dry forests.

Ferns, however, suffered much higher annual losses of up to 20 %. High rates of herbivory among epiphytic ferns were also found in another study in Mexico (Mehltreter et al. 2006). Losses in co-occurring terrestrial ferns were similar. The higher attractiveness of ferns compared to angiosperms seems to be due to their higher nutritional value and better palatability, since mean leaf area loss was positively correlated with leaf nitrogen content (Winkler et al. 2005b).

Schmidt and Zotz (2000) report a local outbreak of caterpillars of *Napaea eucharilla* (Riodinidae, Lepidoptera), which killed 50 % of all *Vriesea sanguinolenta* plants in a local population in lowland Panama. Background levels of herbivory during this three-year study were in line with the typical values of epiphytes mentioned above, i.e., c. 1.7–4.4 % a^{-1}. Although probably exceptional for epiphytes, such observations highlight that there are more facets to herbivory in epiphytes than normally appreciated. Mammals like the Andean bear regularly feast on epiphytic bromeliads (Goldstein 2004) as do monkeys like the capuchins (Fragaszy et al. 2015). Possibly more important than folivory by mammals and other animals is the consumption of reproductive structures, which are typically richer in nutrients. There are reports of damage on flowers (e.g., Cascante-Marín et al. 2009; Aguilar-Rodríguez et al. 2014), fruits (e.g., Ackerman 1989), and flower/fruit stalks (Winkler et al. 2005b). In most cases, this damage is rather moderate, making it unlikely that population growth is affected to a major extent. In some cases, however, it can be quite dramatic: in a Mexican montane forest, about 90 % of developing fruits of the orchid *Lycaste aromatica* were damaged, which was directly linked to low recruitment in this species by Winkler et al. (2005b).

By attracting aggressively foraging ants, extra-floral nectaries (EFN) may be instrumental in protecting reproductive structures from such damage—there are suggestive observations for a few orchids (*Caularthron* and *Schomburgkia* sp., Fisher 1992; Rico-Gray 1989). Interestingly, the percentage of epiphytic species with EFNs within Orchidaceae is higher than expected from their taxonomic contribution (82 % vs. 66 %, compare Keeler 2014 vs. Zotz 2013). Whether this reflects a biased database on the occurrence of EFNs or represents a real difference between life forms could be the subject of future investigations.

Most of the herbivores attacking epiphytes, which have been identified to date, belong to the orders Lepidoptera and Coleoptera (Frank 1999; Schmidt and Zotz 2000; Fisher 1992; Rico-Gray 1989). Notably, the single most important herbivore of Neotropical forests, leaf-cutter ants, seem to shun epiphytes, although casual observations indicate that limited damage may occur in rare cases (G. Zotz, unpubl. obs.).

Insects may also attack stem and meristematic tissue of epiphytes, but the magnitude of this damage has very rarely been quantified (Winkler et al. 2005b). Frank (1999) asserts that the potential for serious damage is limited to those cases of involuntary introduction to new regions (e.g., the weevil *Metamasius callizona* to Florida, Chap. 10) and to epiphyte populations that are already highly stressed for other reasons.

In summary, although the available studies can hardly capture the true complexity of the damage inflicted on epiphytes by herbivorous animals, results are generally in line with theory: herbivory levels are relatively low in epiphytes.

8.3.2 Pollination

Darwin was probably the first to propose that pollinators may be important drivers of speciation. After more than 150 years, the interest in the potential role of plant–pollinator mutualisms in evolutionary processes has not faded, nor has the interest in associated ecological processes such as pollinator vs. resource limitation (Ackerman and Montalvo 1990; Knight et al. 2005). A rich body of literature, which deals one way or another with pollination in epiphytes, has accumulated. (The consequences of different pollination systems for the population biology of vascular epiphytes were already discussed in Chap. 6.)

Fig. 8.3 Bee pollination of orchids. Male euglossine bees have modified legs in which volatile compounds collected from orchid flowers are stored. Many orchid species are exclusively pollinated by male orchid bees. The picture shows two male *Euglossa tridentata* visiting a flower of *Mormodes powellii* in Sierra Llorona, Colón, Panama. (Photograph: David Roubik)

Fig. 8.4 A fair number of bromeliads and other epiphytes are pollinated by hummingbirds. The picture shows the saw-billed hermit (*Ramphodon naevius*) hovering in front of *Aechmea nudicaulis*. (Photograph: Marlies & Ivan Sazima)

Fig. 8.5 Many Bromeliaceae are pollinated by bats. The picture from Bocas del Toro, Panama, shows *Glossophaga commissaris* pollinating *Werauhia gladioliflora*. Note the exposed styles and stamens and the pollen on the bat's forehead. (Photograph: Marco Tschapka)

Members of the Orchidaceae (Tremblay et al. 2005) and Bromeliaceae (Canela and Sazima 2003) have received particular attention, whereas there is rather limited information for other groups, e.g., Gesneriaceae (Borgella et al. 2001), Araceae (Chouteau et al. 2008), or Cactaceae (Cestari and Pizo 2008). For the majority of orchid species, the number of pollinators is small; in the extreme case, there is only one known pollinator (Tremblay et al. 2005; Ackerman and Roubik 2012). Ackerman and Roubik (2012) analyzed data collected over 30 years in the lowlands of Panama and found that the median number of euglossine bees pollinating an orchid species was 3 with a range from 1 to 19 bee species (Fig. 8.3). Generally narrow associations could be a mechanistic explanation for the enormous number of orchid species—an adaptive radiation for specific pollinators caused by selection for outcrossing. However, a test of this notion by Gravendeel et al. (2004) found no statistical support for an association of orchid species richness at the subfamily level and pollinator specialization.

As an ecological consequence, high pollinator specialization and low population densities are probably responsible for low pollination rates and thus low fruit set typical for non-autogamous orchids (Neiland and Wilcock 1998). Among bromeliads, pollination by vertebrates predominates over that provided by insects. Pollination by hummingbirds is common (Fig. 8.4, Kessler and Krömer 2000), and bat pollination has also been reported for species of several genera (Fig. 8.5, Fleming et al. 2009). Overall, the plant–pollinator relationships are not as narrow as in orchids. These more diverse constellations are suitable for testing general ecological and evolutionary theory. For example, Krömer et al. (2008) found significant differences in nectar composition as a function of pollinator preference rather than phylogenetic relationships, and Rocca and Sazima (2013) used hummingbird-pollinated *Vriesea rodigasiana* (Bromeliaceae) to test the assumption that flowers will be positively selected by the most frequent and effective pollinators.

8.3.3 Dispersal

Since most epiphyte species are anemochorous, the role of animals in dispersal is overall smaller in epiphytes than in, e.g., co-occurring trees or climbing plants. However, there are a number of species-rich epiphyte taxa that depend on animals for dispersal (e.g., Araceae, Cactaceae, Ericaceae, Gesneriaceae, Piperaceae, or (in part) Bromeliaceae), and many aspects of their ecology such as spatial distribution patterns can hardly be understood without knowledge of their dispersers. For most groups, the available information is very sketchy (e.g., García-Estrada et al. 2012; Davidson 1988), but some cases are relatively well studied. For example, several studies on taxa with sticky berries (*Rhipsalis* spp., *Anthurium* spp., also mistletoes) suggest that these plants have their own set of avian dispersers (e.g., Snow 1981). The association of these plant groups with frugivorous euphonias in the Neotropics is relatively well understood (e.g., Guaraldo et al. 2013), and an extension to other plant groups (e.g., *Aechmea* spp.) is frequently allured to, but still unsubstantiated. There is some information on bats (Galindo-González et al. 2000; Schlumpberger et al. 2006) or other arboreal mammals (Fontoura et al. 2010) as dispersers of epiphytes.

A few studies investigate the role of ants for epiphyte dispersal, but virtually all of them focus on epiphyte species from ant gardens (see below and, Orivel and Leroy 2011), one of the few exceptions being a report on *Dendrobium insigne* dispersal by an ant species in Papua New Guinea (Benzing and Clements 1991).

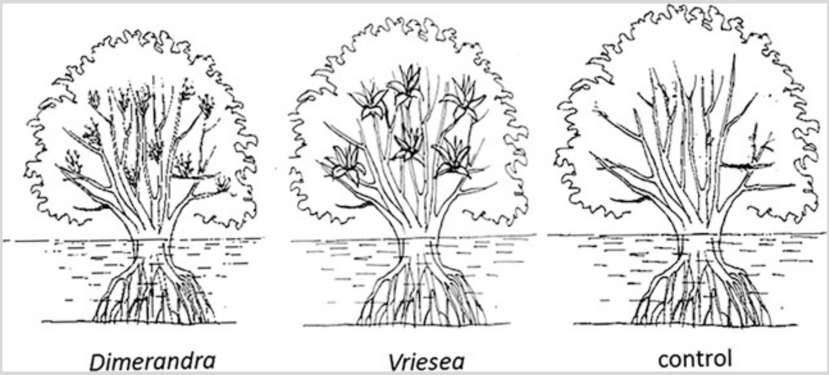
8.3.4 Diffuse Interactions

Negative impacts of arboreal fauna on epiphytes are not restricted to trophic interactions. Perry (1978), e.g., observed that the upper side of limbs of large rainforest trees in Costa Rica is frequently free of epiphytes (Fig. 7.9d). He related this to the activity of arboreal mammals such as white-faced and howler monkeys which use these limbs as major foraging routes. It remains debatable if this really constitutes a major impact on epiphyte assemblages as claimed by Perry (1978), but a test of this notion would be straightforward.

In contrast, the presence of epiphytes positively affects canopy fauna in many ways: by increasing structural diversity in tree canopies (e.g., Hénaut et al. 2014), by offering shelter and nesting space for numerous invertebrates and vertebrates (e.g., Cestari 2009), by affecting microclimatic conditions via local transpiration and shading (Scheffers et al. 2014; Stuntz et al. 2002a), or by creating completely new habitat types (e.g., phytotelmata; see Sect. 8.3.6).

Quantitative evidence for the impact of epiphytes on canopy fauna has accumulated at the level of the individual epiphyte up to the level of entire tree crowns. A particularly informative example is a removal experiment in temperate rainforest in Chile, where large canopy trees were stripped of all epiphytes and compared with intact controls in terms of their invertebrate fauna over an entire year (Díaz et al. 2012). These authors found substantial, quantitative, and qualitative differences: invertebrates were both more species-rich (+60 %) and more abundant (+2000 %) in control trees, functional groups differed (e.g., detritivores were—unsurprisingly—only found in controls), and seasonal variation in abundance differed also. In another study with a similar time frame, Stuntz (2001) studied the impact of structural diversity on spiders in tree crowns. She found significant differences in species and guild composition in tree crowns inhabited by monospecific epiphyte assemblages vs. “empty” trees (Box 8.1). Later studies confirmed this result in a different setting (Goncalves-Souza et al. 2010), prompting these authors to call epiphytes “biodiversity amplifiers.” Further evidence for the key role of epiphytes for canopy invertebrates is provided by Angelini and Silliman (2014) who studied *Tillandsia usneoides* on live oak. Their experimental removal showed that the presence of just one epiphyte species results in an increase in invertebrate species richness by 70 % and in density by 1500 %.

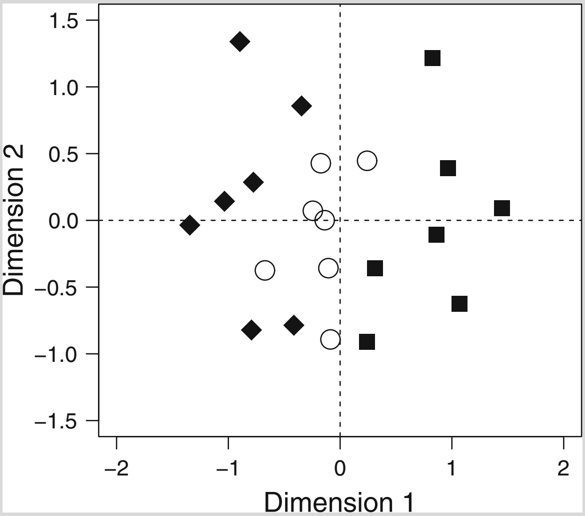
Box 8.1. Epiphytes and Spider Assemblages (Sabine Armsen and Gerhard Zotz)
The influence of epiphytes on canopy arthropods can be studied at different scales, from the level of individual epiphytes up to the level of entire tree crowns. Stuntz et al. (2002b) found significant differences in spider assemblages directly associated with structurally distinct epiphytes (*Dimerandra emarginata* and *Vriesea sanguinolenta*). Here, data are presented from a 13-month sampling campaign in *Annona glabra* crowns with monospecific epiphyte assemblages (7 trees each) and 7 control trees without epiphytes (detailed methodology in Stuntz et al. 2003).



A multidimensional scaling analysis based on the dissimilarities between trees (1- Sørensen) clearly separates spider assemblages in the three tree categories: trees with *D. emarginata* (filled diamond), trees with *V. sanguinolenta* (filled square), and controls without epiphytes (open circle). Differences were also detected in guild structure. For example, trees with the orchid *D. emarginata* had more web builders than controls, while nocturnal and day-active hunters were most numerous in trees with *V. sanguinolenta*. These differences can be directly linked to structural differences. Hunting spiders are known to benefit from litter, which accumulates in phytotelmata, while the long stems of orchids promote web builders. A detailed presentation of all results can be found in Stuntz (2001).

(continued)

Box 8.1 (continued)



There are close to 100 published studies which document how birds use epiphytes and parts thereof as important resources apart from food, e.g., as nesting sites, by using seed comas or entire bromeliads as sources of nesting material (Fig. 8.6) or by using epiphyte mats as foraging site (e.g., Cestari 2009; Nadkarni and Matelson 1989). Most reports supply only anecdotal information, but there is direct experimental evidence for a positive effect of epiphytic vegetation at the level of an entire local bird fauna. Cruz-Angón and Greenberg (2005) conducted an epiphyte removal experiment in shade-coffee plantations in Mexico. Plantations with epiphytes maintained much higher bird abundance and diversity than plantations without epiphytes. Other studies provide more insight into the actual mechanism(s) behind this observation. Several studies demonstrate a protective function. For example, Rivera-Milán (1996) reports significantly higher survival of dove and pigeon nests constructed on epiphytes compared to those constructed on bare branches, probably due to visual protection from predators. Other possible mechanisms behind the effect of epiphytes on birds are related to foraging opportunities, which are either created by the epiphytes themselves (flowers, fruits) or indirectly by the invertebrates and vertebrates living in epiphytes, but not in trees devoid of canopy flora (Nadkarni and Matelson 1989).

8.3.5 Ant Gardens and Ant-House Plants

Because of the omnipresence of ants in tropical forest canopies, interactions with these social insects are virtually “unavoidable” for epiphytes. Most of these, however,

Fig. 8.6 Bird use of epiphytes. Bird nests built almost exclusively of vegetative *Tillandsia* by Oropendulas in Mexico (**a**) and of fruit of *Vriesea sanguinolenta* by flycatchers in lowland Panama (**b**). (Photograph (**a**): Thorsten Krömer)

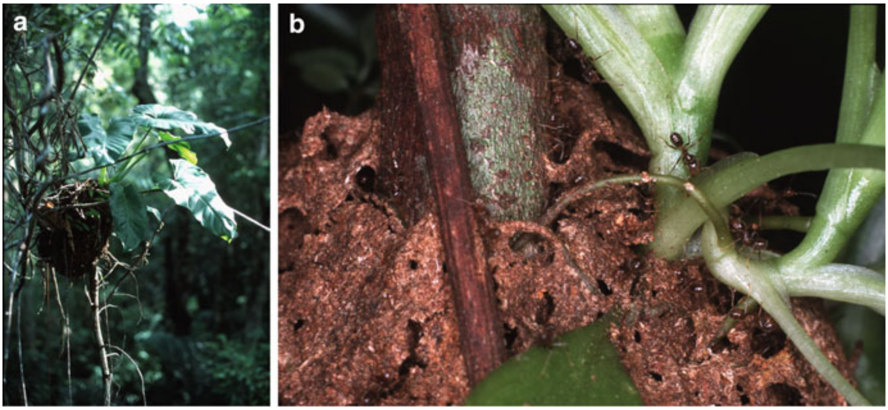


Fig. 8.7 Ant gardens are a classic example of a mutualism between ants and plants (Ule 1901). Shown is an ant garden in a lowland forest in Venezuela (**a**) which is inhabited by a large *Philodendron deflexum* and by *Azteca* sp. (**b**) (Schmit-Neuerburg and Blüthgen 2007). (Photographs: Nico Blüthgen)

are expected to be nonspecific (Yanoviak et al. 2011), but there are two remarkable examples of ant–plant mutualism, namely, ant gardens and ant-house plants.

As already stated by Ule (1901) in his original description of this association, ant gardens (Fig. 8.7) are initiated by the ant partner by building a carton nest, in which plant seeds are deposited. The number of ant species that are able to start an ant garden seems to be quite limited (compare Orivel and Leroy 2011) as is the number of "participating" epiphyte species. There are about 50 species of epiphytes globally that are actively selected by ants using chemical cues on the seed coat. In the

New World, these are basically members of six genera (*Aechmea* and *Streptocalyx*—Bromeliaceae, *Anthurium* and *Philodendron*—Araceae, *Peperomia*—Piperaceae, *Codonanthe*—Gesneriaceae) with a similar number in the Paleotropics (*Dischidia* and *Hoya*—Apocynaceae, *Aeschynanthus*—Gesneriaceae, *Pachycentria*—Melastomataceae, *Poikilospermum*—Urticaceae). Ant-garden species are rarely, if ever, found outside ant gardens (Orivel and Leroy 2011). The nutritional benefit that ants receive from the epiphytes seems to be negligible. The advantage is structural protection (Yu 1994): removing plant foliage exposes the carton during heavy rainstorms. Moreover, the nest further disintegrates when rain-soaked carton remains wet for extended periods and plant roots do not remove moisture.

The epiphyte partner may profit from a mutualistic relationship with ants as a result of effective dispersal (myrmecochory), herbivore protection, or improved nutrition (myrmecotrophy) (Orivel and Leroy 2011). In the case of ant gardens, all three benefits seem to be achieved, which is one of the reasons why Hölldobler and Wilson (1994) called them the "most complex and sophisticated of all symbioses between ants and flowering plants." However, there are no quantitative data on relative costs and benefits. Since the impact of herbivory in epiphytes is assumed to be generally fairly low (Sect. 8.3.1), the main benefit may be nutritional.

Ant-house epiphytes offer living space for these social insects (Fig. 8.8). Again, taxonomic participation is diverse with members of many families, e.g., Apocynaceae, Bromeliaceae, Orchidaceae, Polypodiaceae, or Rubiaceae. Depending on the particular case, cavities of varying complexity are found in swollen stems, rhizomes, or leaves (Fig. 8.8, Gay 1991; Huxley 1978). These cavities either develop autonomously or have to be excavated by the ants. Similar to ant gardens, the main benefit for the plant partners may again be an improved nutrient supply. This has been studied and quantified a few times (e.g., Treseder et al. 1995; see Sect. 5.4).

Although termites may be second in terms of canopy biomass after ants in tropical forest canopies, their biology makes it unlikely that more than occasional interactions with vascular epiphytes occur. Indeed, apart from a few rather casual observations of co-occurrence, e.g., rooting of orchid seedlings in carton trails, there is little indication that this expectation is erroneous (but see, e.g., Flores-Palacios and Ortiz-Pulido 2005).

8.3.6 Phytotelmata and Biotic Diversity in the Forest Canopy

Tank bromeliads hold water, leaf litter, and detritus in their overlapping leaf bases. Such phytotelmata or plant-container habitats provide otherwise rare (e.g., tree holes, Yanoviak 2001) or nonexisting freshwater habitats in tree tops with a rich fauna of both aquatic and soil organisms (Kitching 2000). These water-holding plant structures also offer watering places for arboreal animals, e.g., for birds (Hayes et al. 2009), mammals (Ferrari and Hilario 2012), or termites (Thorne et al. 1996). The biota found inside the tanks encompass bacteria (Giongo

Fig. 8.8 Ant-house plants. (**a**) Modified leaves of *Dischidia* sp. (Apocynaceae). These sac-like leaves are frequently inhabited by ants that deposit debris and raise their young. “ant leaves.” (**b**) Large tuber of *Myrmecodia* (Rubiaceae) which also typically hosts ant colonies—specimen in situ and cross section (**c**) to reveal internal system of connected spaces inhabited by ants. (Photographs: Ulmar Grafe (**a**, **b**), Wilhelm Barthlott (**c**))

et al. 2013), algae (Brouard et al. 2011), carnivorous bladderworts (Fig. 8.9, Taylor 1994), and diverse associations of micro- and macroinvertebrates (Jabiol et al. 2009), but also vertebrates such as anurans (McCracken and Forstner 2014) or salamanders (Ruano-Fajardo et al. 2014). This suggests that the potential importance of epiphytic bromeliads for canopy fauna in Neotropical forests should be even higher than that of large nest ferns in the Paleotropics, where a considerable

Fig. 8.9 "Aquatic" epiphytes. A number of carnivorous bladderworts like the depicted *Utricularia humboldtii* (Lentibulariaceae) can be found growing in bromeliad tanks. (Photograph: Wilhelm Barthlott)

proportion of invertebrate biomass in tree crowns is associated with epiphytes (Ellwood and Foster 2004). Numbers can be impressive: there may be more than 70,000 bromeliads per ha in a cloud forest in Colombia (Sugden and Robins 1979), although densities in lowland forests are usually much lower with, e.g., c. 1000 plants per ha in a wet forest in Panama (Zotz and Schultz 2008). Although few animal taxa are restricted to these phytotelmata, there is even evidence for speciation in this habitat. For example, beetles of the genus *Lachnodacnum* seem to be restricted to phytotelmata (Clarkson et al. 2014) as are a number of protozoans (Foissner 2010). Associations may be quite ancient as indicated by the phylogenetic analyses of Copelatinae diving beetles conducted by Balke et al. (2008): some bromeliad-associated lineages have developed more than 12 MYA ago. All this suggests that we are currently far from a comprehensive understanding of these systems. Not surprisingly then, Dunthorn et al. (2012) note that the number of phytotelmata-endemic ciliates continues to increase as more phytotelmata are sampled and report substantial differences in faunas of bromeliads and other limnetic habitats.

Srivastava et al. (2004) pointed out that these natural microcosms are extremely useful model systems for many ecological questions and, indeed, there is an increasing number of studies using these systems to address a range of questions from the detection of community assembly rules (Armbruster et al. 2002; Petermann et al. 2015), the relative importance of algae as primary producers (Brouard et al. 2011), the relationship of faunal composition and nutrient release (Goncalves et al. 2011), to a possible impact on global climate via methane emissions (Martinson et al. 2010).

8.4 Interactions with Fungi

Considering the general importance of mycorrhizae in nutrient-limited habitats (Smith and Read 1997), vascular epiphytes could be expected to be highly mycorrhizal. In contrast, a recent review suggests the opposite (Brundrett 2009). While

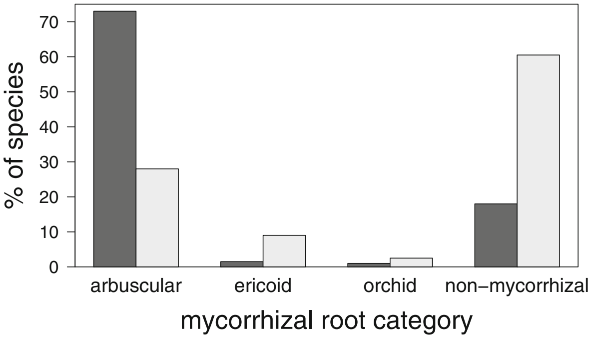


Fig. 8.10 The relative diversity of mycorrhizal or non-mycorrhizal plants in epiphytic habitats (*light gray bars*) compared to plants in non-stressful habitats (*dark gray bars*). Modified after Brundrett (2009)

more than 80 % of all tested terrestrial plant species were mycorrhizal, this was only true for $< 30\,\%$ of all studied epiphyte species (Fig. 8.10). This number does not allow the conclusion that a similarly low percentage of *all* epiphyte species has fungal associates because the absolute number of epiphyte samples is still quite low and, in particular, percentages are not corrected for differences in species numbers among taxonomic groups, e.g., few orchids have been studied. In spite of this caveat, Brundrett (2009) concluded that the relative importance of mycorrhiza is low in "stressful" environments such as arctic, alpine, and epiphytic habitats.

A lower dependence on mycorrhizae for epiphytes would be in agreement with the observation that asymbiotic germination is usually much easier for epiphytic than terrestrial orchids (Dearnaley 2007). Germination in the field, however, seems to require mycorrhizal infection irrespective of habitat, but varying frequencies of mycorrhizae in adult orchids indicate a more mixed picture during later ontogeny (Goh et al. 1992; Lesica and Antibus 1990; Benzing 1981). Overall, however, available data are still rather inconsistent. While many studies, e.g., Kessler et al. (2010) or Muthukumar et al. (2014)'s comparisons of epiphytic and terrestrial ferns, confirm Brundrett´s (2009) conclusions, others disagree. Martos et al. (2012) found no differences in the degree of colonization in a large number of terrestrial and epiphytic orchid species, and Rains et al. (2003) suggested that *all* epiphytic Ericaceae may be mycorrhizal. There is a clear need for more studies with a more balanced representation of all relevant taxa along with a rigorous review of all available data.

Recent evidence also suggests that we should go beyond the study of mycorrhizal symbionts and pay more attention to non-mycorrhizal endophytes. So-called dark septate endophytes (DSEs) may play an important role in ameliorating drought stress, and consistent with this idea a recent study found DSEs to be much more prevalent in epiphytic than terrestrial bromeliads (Lugo et al. 2015).

A final, still unresolved issue in the context of epiphyte–fungus interactions is Ruinen's (1953) notion of "epiphytosis" (Sect. 8.1). The idea that epiphytic plants could damage their host tree via their fungal partner is still untested more than 60 years after its original proposition. If demonstrated at least for a few species or epiphytes with appropriate tracer experiments, such a situation would add an interesting facet of complexity to our view of epiphytic plants.

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The Role of Vascular Epiphytes in the Ecosystem

9

Although the following treatment has a strong tropical bias, it also includes information from the temperate zones—many conclusions should be valid, at least qualitatively, irrespective of latitude. In tropical lowland forests, the biomass of vascular epiphytes is usually much lower than in montane settings. Because of the generally observed decrease in stature and aboveground biomass of tropical forests with elevation (Whitmore 1984; Stadtmüller 1987), which goes along with a similar trend in aboveground net primary productivity of these forests (Weaver and Murphy 1990; Waide et al. 1998), the impact of epiphytes on major ecosystem processes, e.g., the fluxes of water, nutrients, or carbon, should vary substantially with forest type. For example, Golley et al. (1969) estimate that the total biomass of vascular epiphytes in a moist forest in Panama is equivalent to just 0.02 % of the dry mass of tree foliage. On a *total* aboveground biomass basis that proportion would obviously be considerably lower and thus rather negligible as far as carbon and nutrient fluxes are concerned. However, this statement shall not downplay other potentially important biological roles of epiphytes in lowland forests, e.g., in relation to the canopy fauna via melioration of climatic extremes (Stuntz et al. 2002; Freiberg 2001, Chap. 8). Nonvascular epiphytes show even more pronounced altitudinal increases in biomass (Frahm 1990). Thus, in the lowlands they are rarely considered important enough as to be included in biomass assessments (but see Freiberg and Freiberg 2000).

The large epiphytic component of many montane rainforests leaves little doubt about a substantial influence on ecosystem functioning (Table 9.1). Although the altitudinal increase in biomass of nonvascular epiphytes generally exceeds that of vascular epiphytes, functional relevance is not restricted to epiphytic mosses and lichens. On average, the vascular component of living epiphyte biomass accounts for c. 30 % of the total epiphytic biomass in the studied forests, with some estimates of vascular epiphyte biomass for montane rainforests in Costa Rica and Colombia exceeding 8000 kg ha^{-1}. Neither mean annual temperature (MAT), mean annual precipitation (MAP), nor the combination of both explains a major portion of the observed variation in biomass of vascular epiphytes (regression models $p > 0.05$

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Table 9.1 Vascular epiphyte biomass in forests in tropical, subtropical, and temperate latitudes

Forest type	Country	Elevation	Latitude	S/N	Epiphyte biomass (kg ha^{-1})	% total epiphyte biomass	% tree foliage	Source	Comments
Dry forest	Puerto Rico	<10 m asl	17	N	140			Murphy and Lugo (1986)	
Moist forest	Panama	Lowland	8	N	2			Golley et al. (1969)	
Gallery forest	Panama	Lowland	8	N	30			Golley et al. (1969)	
Mangrove	Panama	Lowland	8	N	21			Golley et al. (1969)	
Moist forest	Panama	40 m asl	9	N	70			Zotz (2004)	0.4 ha of forest
Moist forest	Brazil	Lowland	3	S	c. 50			Klinge et al. (1975)	
Redwood forest	USA	60 m asl	41	N	421		0.5	Sillett and Van Pelt (2007)	Many accidental species
Temperate rainforest	USA	ca. 100 m asl	47	N	549	9.7	10	Nadkarni (1984a)	
Submontane moist forest	Brazil	200 m asl	25	S	5339			Petean (2009)	Only vascular epiphytes studied
Premontane	Panama	250—600 m asl	8	N	1440		14	Golley et al. (1969)	
Subtropical wet forest	Taiwan	400 – 1400 m asl	24	N	1273	42.3	5	Hsu et al. (2002)	
Montane forests	Mexico	720 m asl	19	N	270			Hietz and Hietz-Seifert (1995)	Only holoepiphytes
Premontane floodplain forest	Puerto Rico	750 m asl	18	N	1400			Frangi and Lugo (1985)	Primarily *Guzmania berteriana*
Moist lower montane forest	Brazil	900 m asl	25	S	472		13	Socher et al. (2008)	
Montane forests	Mexico	1000 m asl	19	N	940			Hietz and Hietz-Seifert (1995)	Only holoepiphytes

Montane forests	Mexico	1370 m asl	19	N	62			Hietz and Hietz-Seifert (1995)	Only holoepiphytes
Submontane rainforest	Tanzania	1400 m asl	7	S	174	8.9	0.2	Pócs (1980)	
Montane forests	Mexico	1430 m asl	19	N	2500			Hietz and Hietz-Seifert (1995)	Only holoepiphytes
Lower montane forest	Costa Rica	1480 m asl	10	N	8205	66.9		Nadkarni et al. (2004)	Old-growth forest
Lower montane forest	Costa Rica	1500 m asl	10	N	2615	18.5		Köhler et al. (2007)	Old-growth forest
Elfin cloud forest	Costa Rica	1600 m asl	10	N	710	27.2	30	Nadkarni (1984b)	Biomass calculated from original figures
Montane rainforest	Jamaica	1600 m asl	18	N	260 - 1500		38	Tanner (1980)	Only bromeliads, range of two plots
Montane rainforest	Thailand	1700 m asl	18	N	2800	42.0	12	Kanzaki and Sri-ngernyuang (2012)	Extrapolated from a single tree
Montane forests	Mexico	1980 m asl	19	N	290			Hietz and Hietz-Seifert (1995)	Only holoepiphytes
Montane rainforest, ravines	Ecuador	2000–2200 m asl	3	S	126	12.32		Werner et al. (2012)	
Montane rainforest, mid-slope	Ecuador	2000–2200 m asl	3	S	1174	61.8		Werner et al. (2012)	
Montane rainforest, ridge-top	Ecuador	2000–2200 m asl	3	S	1422	65.1		Werner et al. (2012)	
Mossy elfin forest	Tanzania	2120 m asl	7	S	897	8.9	11	Pócs (1980)	

(continued)

Table 9.1 (continued)

Forest type	Country	Elevation	Latitude	S/N	Epiphyte biomass (kg ha^{-1})	% total epiphyte biomass	% tree foliage	Source	Comments
Montane forests	Mexico	2370 m asl	19	N	150			Hietz and Hietz-Seifert (1995)	Only holoepiphytes
Montane rainforest	New Guinea	2500 m asl	6	N	1060		22	Edwards and Grubb (1977)	Average of six plots
Montane rainforest	Venezuela	2400–2800 asl	8	N	9865			Walker and Ataroff (2002)	
Upper montane rainforest	China	2600 m asl	24	N	234	12.3		Chen et al. (2010)	Only ferns
Upper montane rainforest	Colombia	2700 m asl	4	N	1130	30		Caballero-Rueda et al. (1997)	
Upper montane rainforest	Costa Rica	2900 m asl	9	N	705	26.8	7	Hölscher et al. (2004)	
Montane rainforest	Costa Rica	2900 m asl	9	N	770	24.4		Köhler et al. (2010)	Old-growth forest
Upper montane rainforest	Colombia	3370 m asl	4	N	4059	34.1		Veneklaas et al. (1990)	Dominant *Weinmannia* trees
Montane rainforest	Colombia	3700 m asl	7	N	8685	53.4	24	Hofstede et al. (1993)	Extrapolated from 3 trees

and $r^2 \leq 0.08$). This contrasts with bryophytes in the same forests. Their biomass shows a negative trend with increasing MAT and a positive relationship with MAP (multiple regression, $p < 0.01$ and $r^2 = 0.44$).

It is instructive to compare the biomass of vascular epiphytes with estimates of the green biomass of co-occurring trees. On average, vascular epiphyte biomass is equivalent to about 20 % of tree foliage in the studied montane forests (Table 9.1). Such a comparison is still potentially misleading because only a part of epiphyte biomass is productive, yet available publications do not always distinguish between epiphyte leaves, roots, and stems. For example, although Nadkarni et al. (2004) report c. 8000 kg ha^{-1} for living epiphytic biomass, just 10 % of this represents photosynthetically active organs. Unfortunately, different and functionally diverse components, i.e., nonvascular and vascular epiphytic biomass, dead organic material, tree foliage, or total forest biomass, are sometimes mixed up and incorrect statements are not infrequent in the literature. Confusion could be reduced by using the terms "epiphytic matter" to refer to all organic material, life or dead, and restrict the use of the term "epiphyte biomass" to living plant parts. Comparing data for green tissue of vascular epiphytes and tree foliage suggests that ca. 10 % is a typical value (Table 9.1). In the exceptional case, however, the foliage of vascular epiphytes can exceed that of the host tree as reported for a *Eucryphia cordifolia* tree growing in a cool temperate rainforest in Chiloé, Chile (Díaz et al. 2010).

The compiled values were obtained using a number of different methodologies. Some are based on just one or very few emergent trees and were still extrapolated to an entire forest (e.g., Hofstede et al. 1993; Kanzaki and Sri-ngernyuang 2012). Since epiphytic biomass accumulates over time (Díaz et al. 2010), this approach is likely to lead to overestimates, because smaller trees will have much lower epiphyte loads. Quantitative evidence for this statement is available from comparisons of the epiphyte load of individual trees of varying size within a given forest (Fig. 9.1) as

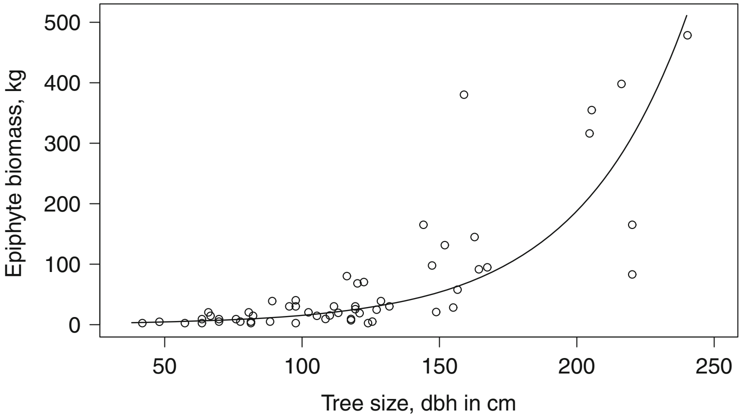

Fig. 9.1 Relationship between trunk diameter at breast height (dbh, cm) of *Eucryphia cordifolia* trees and biomass of vascular and nonvascular epiphytes (kg) in forests on Chiloé Island, Chile. The *solid line* suggests an exponential relationship of dbh and biomass ($r^2 = 0.6$). Modified after Díaz et al. (2010)

well as for forests as a whole, e.g., in comparisons of primary and successional forests: epiphytic matter (= living biomass and canopy humus) in old-growth forests in Costa Rica was between 20-fold to >40-fold higher compared to c. 30-year-old secondary forests (Köhler et al. 2007; Nadkarni et al. 2004). In the following sections, I will summarize the available evidence for the importance of vascular epiphytes on carbon fluxes, on hydrological processes, as well as on nutrient storage and fluxes in the ecosystem.

9.1 Carbon Stores and Carbon fluxes

Productivity

The combined green biomass of vascular and nonvascular epiphytes can come close to the biomass of tree foliage in some forests, the highest figure for vascular epiphytes *alone* being 38 % at the plot level (Tanner 1980, Table 9.1) or >100 % at the tree level (Díaz et al. 2010). However, pools and fluxes should not be confused (Leuzinger and Haettenschwiler 2013). Hence, these findings are not indicative of a proportional contribution of epiphytes to primary productivity. Indeed, the reported values of maximum rates of CO_2 uptake (A_{max}) compiled in Table 9.2 show that even under favorable conditions the capacity of epiphytic leaves to fix carbon is lower than that of tree foliage. On average, mass-based A_{max} of vascular epiphytes amounts to just 70 % of trees, whereas A_{max} of mosses and lichens is even lower, e.g., just about 20 % in the case of bryophytes. Considering that epiphytes should be much more affected by water shortage than trees, the integrated carbon gain is expected to be lower still. A case study in which leaf gas exchange of epiphytic and ground-rooted individuals of *Clusia uvitana* were compared over the course of an entire year allows us to quantify this effect (Zotz and Winter 1996). The maximum rates of CO_2 uptake of epiphytic plants were c. 30 % lower, but the estimated annual carbon budget was reduced by more than 40 % compared to hemiepiphytic individuals. The discrepancy between A_{max} and long-term carbon gain is probably even more pronounced in nonvascular epiphytes due to their poikilohydric nature. The tight correlation of A_{max} and daily carbon gain in vascular plants (integrated CO_2 gain $= 20 \times A_{max} - 2.1$, Zotz and Winter 1993) indicates average rates of CO_2 uptake of about 50 % A_{max}. For nonvascular plant,

Table 9.2 Dry mass-related rates of maximum net CO_2 uptake in tropical trees, vascular epiphytes and nonvascular epiphytes (mosses, and lichens) compiled from a variety of sources

Life form	Number of species and region	A_{max} (nmol CO_2 g^{-1} s^{-1})
Trees	29 species from Panama and Venezuela	87.8 ± 30.4
Vascular epiphytes	12 species from tropical America and Asia	67.7 ± 32.7
Epiphytic bryophytes	20 species from Panama (montane)	19.2 ± 15.7
Epiphytic lichens	12 species from Panama (lowland / montane)	37.2 ± 29.4

Only field measurements were considered. Data from the GLOPNET data base for vascular plants and from other sources for nonvascular epiphytes

Table 9.3 Standing crop and productivity estimates for three forest types in Luquillo Experimental Forest in Puerto Rico

Forest type	Tabonuco	Palo Colorado	Dwarf forest
Forest above-ground biomass (Mg ha^{-1})	197.9	135.8	82.9
Forest leaf biomass (kg ha^{-1})	7900	5800	2900
Bromeliad biomass (kg ha^{-1})	1.2	111	550
% Forest leaf biomass	0.02	1.9	19
Forest net primary productivity (NPP, kg ha^{-1} y^{-1})	10500	7600	3700
Bromeliad productivity (kg ha^{-1} y^{-1})	0.42	38.8	474.1
% Forest NPP (bromeliads/total)	0.004	0.51	12.8

Data from Richardson et al. (2000), and Weaver and Murphy (1990)

on the other hand, Elbert et al. (2012) propose a scaling factor of 1/3 × ¼, i.e., only 8 %, to obtain estimates of carbon gain from known $A_{\max}$ values.

The contribution of vascular epiphytes to forest primary production (NPP) has rarely been directly quantified, an exception being Richardson et al.'s (2000) study in Puerto Rico. These researchers focused on epiphytic bromeliads, which showed a dramatic increase in densities from lower montane forests to montane dwarf forest, where densities exceeded 30,000 individuals ha^{-1} (Table 9.3). Using Weaver and Murphy (1990) data on forest biomass and NPP from the same systems, they arrived at an estimate of almost 13 % of NPP attributable to these epiphytes. In the two other forests, however, the contributions of epiphytic bromeliads to forest NPP were rather negligible. In conclusion, current evidence suggests that the contribution of vascular epiphytes to NPP in forest ecosystems is quite low in all but the exceptional case.

Litter fall

There are several studies with data on epiphyte litter fall (e.g., Tanner 1980; Oliveira 2004), but Nalini Nadkarni and her group have probably produced the best data sets on epiphyte litter fall and dynamics so far. Annual epiphyte litter fall in a Neotropical cloud forest in Monteverde, Costa Rica, amounted to 500 kg ha^{-1}, compared to 7000 kg ha^{-1} produced by trees (Nadkarni and Matelson 1992). Only a tiny fraction, <1 %, of total litter was retained in tree crowns (Nadkarni and Matelson 1991). The accumulated litter mass on the ground was comparable to the annual input. Assuming steady-state conditions in this old-growth forest, the annual decay rates of epiphyte-derived litter were considerably higher than those of litter derived from terrestrially rooted plants. However, the epiphyte litter fraction encompassed very heterogeneous groups, i.e., fast-decomposing bryophytes on the one hand and vascular plant, which fell as intact plants and may stay alive for years before they die and start to decompose (Matelson et al. 1993), on the other hand. Apart from the substantial lag time between litter fall and decomposition, Nadkarni and Matelson (1992) also observed a difference in the spatial distribution of epiphyte litter compared to litter from terrestrially rooted flora. While the latter is more or less evenly distributed across the forest floor, epiphyte litter frequently occurs in big mats with a very patchy spatial distribution, which must result in a very localized release of nutrients. This patchiness in litter fall is also a plausible reason for the much lower estimates of epiphyte litter fall by earlier studies (e.g., Tanner 1980) that used relatively small litter fall collectors.

9.2 Forest Hydrology

Both vascular and nonvascular epiphytes can affect the hydrological regime of forests via interception, storage and (evapo)transpiration (Holwerda et al. 2013). A number of hydrological studies have quantified the role of epiphytes (e.g., Veneklaas and Van Ek 1990; Pócs 1980; Köhler et al. 2007), but few have tried to tease apart the effects of vascular epiphytes, nonvascular epiphytes, and accumulated dead organic material on forest water fluxes. Hence, our understanding of the individual effects of different groups of epiphytes on the spatial and temporal variation of throughfall and its chemistry is still quite poor (Levia and Frost 2006). In spite of some additional research in subsequent years, a recent review does not really come to different conclusions: Van Stan and Pypker (2015) identify important knowledge gaps and state that the role of *vascular* epiphytes has received particularly little attention.

In his classic study on the epiphytes of the Uluguru Mountains in Tanzania, Pócs (1980) documented a dominant role of so-called microepiphytes (mostly bryophytes). Although their biomass in a mossy elfin forest exceeded that of tree foliage by just 20 %, their interception capacity was > 600 % higher, above 40,000 l ha^{-1} in absolute terms. Vascular epiphytes, equivalent to c. 10 % of tree leaf biomass, intercepted a mere 3 % of the total. Subsequent release of intercepted precipitation is generally very slow. While bare tree bark may drain intercepted moisture within minutes, wet epiphyte mats increase air humidity locally for days (Veneklaas and Van Ek 1990; Köhler et al. 2007). There seems to be a consensus that *vascular* epiphytes usually play a rather minor role in forest hydrology, in contrast to *nonvascular* epiphytes, particularly bryophytes. Even in the case of the dwarf forest studied by Richardson et al. (2000) with very high densities of bromeliad tanks, their water storage capacity amounted to only 3300 l ha^{-1} or 0.3 mm of rain. Trunk-dwelling epiphytes should affect stemflow and, indeed, Oyarzun et al. (2011) found a significant, negative correlation between epiphyte cover and stemflow in an old-growth evergreen forest in the Andes of South-central Chile.

In lowland forests, saturation storage capacities of the forest canopy are generally ≤ 1 mm (Jetten 1996). In montane forests, on the other hand, a *potential* storage capacity of 5 mm is not unusual, most of which is directly related to the larger epiphyte loads (Veneklaas and Van Ek 1990; Köhler et al. 2007; Pócs 1980). However, such numbers are of limited value to predict the *actual* storage capacity on any given day, because the latter depends on the balance of previous inputs and losses (Köhler et al. 2007), and interception does not only depend on storage capacity either—naturally, its proportion is inversely related to the amount of precipitation during a rain event. An analytical model developed by Hölscher et al. (2004) for an upper montane rainforest in the Cordillera de Talamanca, Costa Rica, suggested that the average contribution of (nonvascular) epiphytes to total interception is only 6 %. The results of long-term studies, which directly determined interception in other epiphyte-rich forests, are at odds with such a low value. Estimates of annual interception range from 12–16 % in montane rainforests in Mexico or Colombia (Veneklaas and Van Ek 1990; Munoz-Villers et al. 2012) to 40–50 % in two lower montane rainforests in Panama and Ecuador (Cavelier et al. 1997; Fleischbein et al. 2005).

The interception of fog and cloud water represents an additional, potentially important source of water. Such "occult precipitation" can be substantial. In the extreme case, annual fog interception may rival the input by precipitation (Cavelier and Goldstein 1989; Weaver 1972), although even in montane settings typical values are much lower (5–30 %, Wallace and McJannet 2013) or of clearly marginal importance (<2 %, Munoz-Villers et al. 2012; Cavelier et al. 1997). The great potential of occult precipitation to affect vegetation structure becomes apparent in many cloud forests. In spite of the already high amounts of rainfall, there is no doubt that the marked increase in epiphyte richness and abundance on windward compared to leeward slopes, which is consistently reported from forests in the Caribbean, e.g., from Costa Rica, Colombia, or Venezuela, is associated with frequent immersion in clouds (Sugden 1986).

9.3 Nutrient Stores and Fluxes

The contribution of epiphytes to nutrient stores is higher than expected from their biomass (Table 9.4). The compiled data sets indicate that, e.g., N is enriched about two- to threefold in vascular epiphytes, which is not entirely surprising considering the much larger proportion of green, productive, N-rich tissues (10–30 % plant^{-1}) compared to the dominant trees, where leaves account for only 1–2 % of the total biomass (Nadkarni et al. 2004; Hsu et al. 2002). These nutrients are only temporarily immobilized in canopy-held organic matter (Hietz et al. 2002). Sooner or later they are bound to take part in the biogeochemical cycles of the entire ecosystem. Figure 9.2 depicts the different pools and fluxes. Inevitably, epiphytes alter nutrient fluxes in the ecosystem in time and space (Reynolds and Hunter 2004; Benzing and Seemann 1978; Nadkarni et al. 2004), but the crucial questions are how large this effect really is and whether epiphytes generate a substantial net gain for their host trees or, alternatively, scavenge nutrients to a degree that the trees are negatively affected. A number of studies supply parts of the answers, but none provides the complete picture: one would need research that quantifies the different fluxes and changes in pool sizes shown in Fig. 9.2 over prolonged periods, combined with manipulations such as epiphyte removal.

One extreme standpoint has been taken by Benzing and Seemann (1978), who called epiphytes "nutritional pirates." They argued that epiphytes scavenge nutrients making them unavailable to the host tree for extended periods of time.

Table 9.4 Proportional contribution of different structural components to forest biomass and nutrient capital

Forest compartment	Biomass	N	P	K	Ca	Mg
Upper montane forest, New Guinea						
Trees	89	69	61	82	78	77
Other ground-rooted plants	4	10	11	12	8	9
vascular epiphytes	0.6	1.8	2.5	1.6	1	1.6
Epiphyte soil	0.6	3.5	2.5	0.5	0.7	1.1
Forest floor	6	16	22	4	13	12
Lower montane moist forest, Costa Rica						
Trees	92.8	86.8	89.0	94.4	93.8	94.5
Other ground-rooted plants	0.9	2.7	2.3	1.9	1.3	1.3
Nonvascular epiphytes	0.8	1.3	1.1	0.4	0.6	0.5
Vascular epiphytes	1.6	2.6	2.1	0.9	1.2	1.0
Epiphyte soil	4.0	6.6	5.5	2.3	3.1	2.6
Subtropical premontane forest, Taiwan						
Trees	98.8	95.7	97.2	95.5	98.3	97.3
Nonvascular epiphytes	0.6	2.2	1.4	2.3	0.9	1.4
Vascular epiphytes	0.5	1.6	1.1	1.7	0.7	1.0
Epiphyte soil	0.1	0.4	0.3	0.5	0.2	0.3

Data in each column are percentages. The different studies use somewhat different categories, which does not hamper overall comparability. Sources are: Grubb and Edwards (1982): New Guinea, Nadkarni et al. (2004): Costa Rica, Hsu et al. (2002): Taiwan

Alternatively, there may be a measurable benefit for the host tree, when epiphytes increase the deposition of moisture and solutes (e.g., Clark et al. 1998; Knops et al. 1996; Stanton et al. 2014). For example, by experimentally removing epiphytic lichens from oak trees, Knops et al. (1996) showed that intercepted precipitation was reduced by 50 % in lichen-stripped trees with reduced concentrations of major nutrient elements in throughfall. However, manipulations over three years did not yield an effect on trees, most likely because of large soil nutrient pools. Even in a forest with an extraordinary abundance of bromeliads, the Puerto Rican dwarf forest studied by Richardson et al. (2000), the nutrient capital of living epiphytes proved to be much smaller than, e.g., nutrient pools in litter on the forest floor. A similar picture emerged for nutrient fluxes in the same forest. Estimates of the proportion of the nutrients that flow through these phytotelmata suggest that <10 % of N, Ca, or Mg and c. 25 % of P and K were accumulated in epiphyte tissues. To conclude, there are measureable, often positive effects of epiphytes on forest nutrient cycles, but the effects on the host trees, whether positive or negative, are probably limited in most cases.

Nutrient pools and fluxes in tree crowns with and without epiphytes differ in many regards (Fig. 9.2). About 1 % of the total fine litter fall may be retained in the canopy by epiphytic phytotelmata and other structures (Nadkarni and Matelson 1991). Nutrients released from this litter and additional input from leachates of tree foliage are the most likely explanation for the close correlation of epiphyte

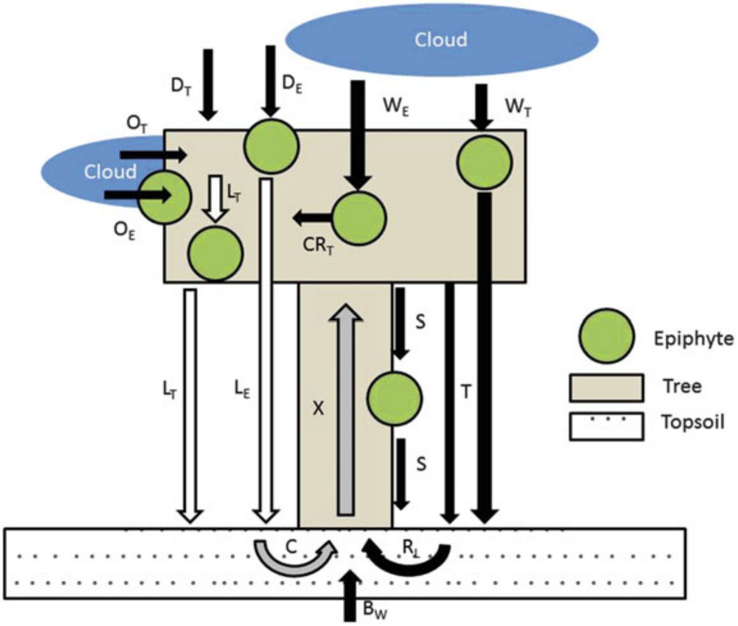

Fig. 9.2 Schematic sketch of nutrient pools (*rectangles* and *circles*) and fluxes (*arrows*) in a forest ecosystem with epiphytes. Input is indicated by *solid arrows* and output (=leaching; L) by *open arrows*. Wet (W), dry (D), and occult (O) deposition, throughfall (T), and stemflow (S) are distinguished. Nutrients may reach the crown also via xylem flow (*gray arrow*), which transports nutrients derived from the bedrock (B), from decomposition of litter (C), and recycling of nutrients (R) from throughfall, leaching, and stemflow. A shortcut is the direct uptake of nutrient pools associated with epiphytes via canopy roots of trees (CR). *Subscripts* indicate whether the epiphyte (e) or the tree (t) are affected

abundance and soil properties in the Central Amazon (Boelter et al. 2014) or the substantial stimulation of epiphyte growth and abundance by experimental soil fertilization (Benner and Vitousek 2007). Another observation associated with the presence of epiphytes in many trees is the growth of adventitious tree roots in epiphyte mats (Herbert 1958; Nadkarni 1981). This observation opened the exciting possibility of a third avenue for nutrient transfer from epiphytes to trees apart from leaching and litter fall. Arguments against its ecological importance have already been discussed in Sect. 8.1. Even if canopy roots are shown to be functional (Orlovich et al. 2013), a glance at pool sizes (Table 9.4) puts the relative importance of canopy organic material into perspective. Nutrients pools in ground litter are at least one order of magnitude larger than those in the canopy (Grubb and Edwards 1982).

A large proportion of the epiphyte mats is made up by dead canopy organic material (DOM), mostly derived from nonvascular epiphytes. Although technically not considered true soils, these accumulations of DOM in tree canopies, with interspersed roots of epiphytes (and of the host tree itself?), along with diverse biota of invertebrates, fungi, and bacteria are frequently called “canopy soils” (“sols suspendus,” Paulian 1951). Reports from both the temperate zone and the tropics show that mineralization in these soils is highly variable in time, but mineralization rates as such seem to be comparable in the canopy and the upper horizons of the forest floor (e.g., Pérez et al. 2005; Vance and Nadkarni 1990). Nitrification, however, is generally suppressed (Pérez et al. 2005; Vance and Nadkarni 1990; Inselsbacher et al. 2007), which is possibly related to the lower pH in the canopy. Since mobility of ammonium is lower than that of nitrate, this may have important consequences for nutrient retention and fluxes in canopy soils. Experiments with stable isotopes such as the ^{15}N pool dilution method developed by Umana and Wanek (2010) offer a possible avenue to study these processes in more detail, allowing a better understanding of the functioning of canopy soils.

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Epiphytes and Humans

10

There is increasing evidence that we are currently experiencing an extinction event of geological magnitude (Barnosky et al. 2011). No doubt, biodiversity is threatened globally by human action. Sala et al. (2000) identified five major drivers of change in biodiversity (Fig. 10.1): while there is still discussion whether ongoing increases in (1) atmospheric CO_2 concentration and (2) associated climatic changes are *entirely* due to human activities, there is no doubt whatsoever who is responsible for (3) pollution, (4) land-use change, and dramatic increases in (5) biotic exchange. All five major drivers of change in biodiversity *in general* also affect epiphytes *in particular*, but land-use changes are arguably by far the most important one (Zotz and Bader 2009), as for tropical biomes in general (Fig. 10.1, Sala et al. 2000). A sixth driver, which is not mentioned by these authors, is “non-sustainable collection” of particular species, i.e., the exploitation of wild populations, for ornamental, cultural, or medicinal purposes. Generally speaking, collections made to meet such demands are probably a much smaller threat to epiphytes than habitat destruction, but local populations of some species (e.g., a number of so-called gray *Tillandsias* or many *Dendrobium* species) may be seriously endangered and need protection (http://www.iucnredlist.org, Liu et al. 2014; Flores-Palacios and Valencia-Diaz 2007).

10.1 Land-Use Change

There are contrasting reports concerning the vulnerability of epiphytes to large-scale land-use changes. On the one hand, Ackerman (2007) emphasizes the resilience of orchids in general. In spite of temporary reduction of forest cover in Puerto Rico by 95 % in the mid-twentieth century, only 5 % of the native orchid flora has been lost. In stark contrast, 60 % of the epiphytes and a stunning 90 % of the orchids went extinct during the urban development of Singapore, compared to just 26 % of the flora in general (Turner et al. 1994). Leao et al. (2014) studied the relationship of extinction risk and (1) vegetation type, (2) geographic range size, and (3) growth

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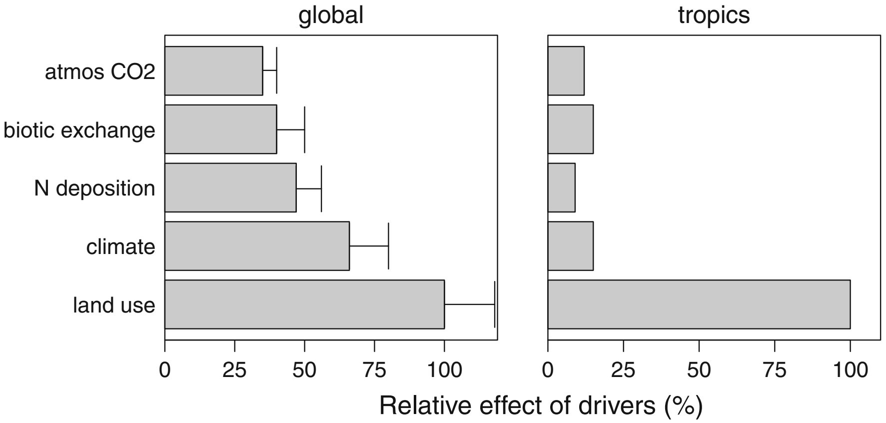

Fig. 10.1 Major drivers of change in biodiversity. Shown is the relative effect of five major drivers compared to that of changes in land use. The *left plot* shows averages (± SE) across biomes; the *right plot* focuses on tropical biomes. It becomes evident that currently the dominance of land-use change as the major threat to biodiversity is particularly strong in the tropics. Modified after Sala et al. (2000)

form in the Atlantic Forest of Brazil. Epiphytes showed the highest extinction risk, but only when phylogeny was ignored. However, does it really make a difference in its ecological consequences that epiphytic bromeliads are not prone to extinction because of being an "epiphyte," but because of being a "bromeliad"? In Neotropical forests, the members of this family are so important ecologically that their demise should have drastic cascading effects for the entire ecosystem (Cruz-Angon et al. 2009). This phylogenetic signal highlights once again a basic, recurring problem mentioned throughout this book: the taxonomic groups included in the three mentioned studies differ very much. Ackerman's (2007) analysis only refers to orchids, a group which is not included in Leao et al.'s (2014) study, while Turner et al. (1994) analyzed an entire local epiphyte flora. Clearly, our current database does not allow any generalization on a particularly pronounced extinction threat of vascular epiphytes compared to other plant groups.

Frequently, "land-use change" is a blunt euphemism for habitat destruction: if larger areas of forest are cleared completely, the destiny of resident epiphytes is obvious (Fig. 10.2). Examples of land-use changes, in which the consequences for epiphytes are less unambiguous, are selective logging activities, conversion of forests to (traditional/shaded) coffee plantations, or other forms of agroforestry (Fig. 10.3). Much land in the tropics is also converted to pastures (Fig. 10.3b), often sparing scattered isolated remnant trees (with epiphytes) as a source of shade for cattle. In the long run, timber plantations or secondary forests, which may develop on previously cleared land that is not used for agriculture, may provide new habitat for epiphytes, although species richness in these forests is usually lower as colonization of young trees is generally a slow process (Krömer et al. 2014; Barthlott

Fig. 10.2 Slash-and-burn agriculture. Habitat destruction is currently the most serious threat to vascular epiphytes (Photograph: Marcos Guerra)

et al. 2001). However, we are just beginning to study the conservation value of such systems for epiphytes, because epiphyte researchers were traditionally more interested in epiphytes in pristine settings. The fact that 60 % of the world's tropical rainforests were already classified as degraded by the year 2000 (International Tropical Timber Organization 2002) has led to a shift in focus. Although still sketchy, there is an increasing body of information on epiphytes from a large number of secondary habitats, e.g., coffee plantations (Hietz 2005; Mondragón et al. 2009), oil palm plantations (Gill and Onyibe 1986), other tree plantations (Boelter et al. 2011), isolated pasture trees (Hietz-Seifert et al. 1995; Poltz and Zotz 2011), or logged forests and other secondary forests in different stages of restoration (Benavides et al. 2006; Cascante-Marín et al. 2008; Krömer and Gradstein 2003). Even isolated trees and parks in urban areas have received some attention in the last few years (Figs. 10.4 and 10.5, Bryan 2011; Adhikari et al. 2012; Izuddin and Webb 2015).

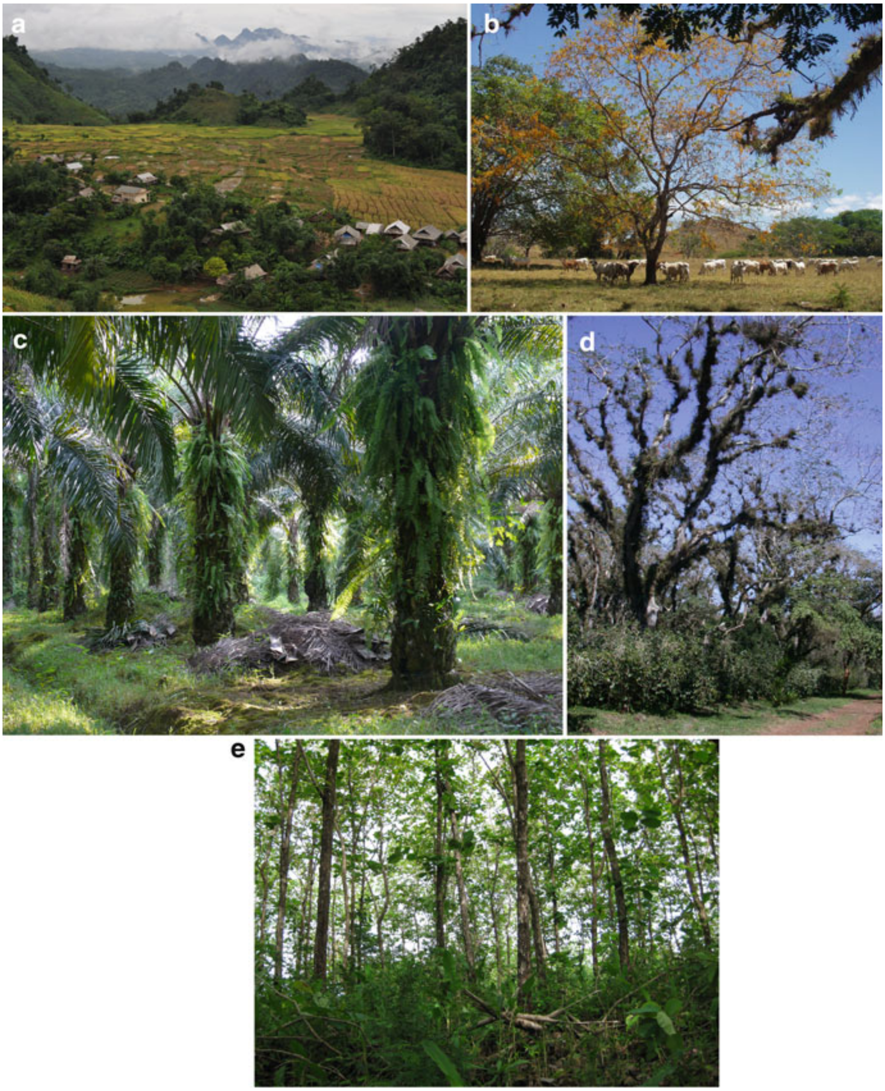

Fig. 10.3 Previously forested landscapes may be converted in many ways. At the landscape level, there may be a mosaic of relatively undisturbed forests with field and human settlements (**a**, Vietnam), but often large areas have been entirely transformed into pastures with scattered trees; (**b**) shows such a landscape in the Azuero peninsula (Panama). Note the lush epiphyte cover (*Tillandsia fasciculata*) on the branches in the foreground. Epiphyte diversity and abundance can vary substantially in different forms of plantations. While at least sometimes relatively rich in some oil palm plantations (**c**) and traditional forms of coffee plantations (**d**), teak plantations (**e**) are frequently “epiphyte deserts”. (Photographs: **a**: Florian Werner, **b**: Kerstin Poltz, **c**: Holger Kreft, **d**: Peter Hietz, **e**: Helena Einzmann)

Fig. 10.4 Epiphytes in urban settings. Shown are trees in downtown Paramaribo (Suriname) loaded with vascular epiphytes

Although the epiphyte assemblages in these human-modified systems are typically qualitatively and quantitatively very different from those found in original vegetation, this is not always the case. For example, old shade trees in traditional coffee plantations host epiphytes in comparable numbers to forest trees (Hietz 2005), while structurally impoverished tree plantations with exotic Pine or Eucalypt species are usually deprived of most epiphytes which can be found in nearby forest fragments (Fig. 10.6, Boelter et al. 2011). In contrast to the general trend described above, trees in disturbed forests or isolated remnant trees in cattle pastures may sometimes have epiphyte assemblages comparable to those of primary forest in terms of species numbers (Larrea and Werner 2010; Hietz-Seifert et al. 1995). Typically, however, hygrophilous filmy and grammitid ferns and other understory taxa are the first to suffer from habitat alterations and resulting changes in microclimate, while more xerophytic taxa may even benefit. As a case in point, Krömer et al. (2013) and Armenta-Montero et al. (2015) show that 72 % of grammitid ferns and all *Phlegmariurus* species from Veracruz, Mexico, belong to a threatened category considering the IUCN regional criteria, mainly because of the continuous loss and fragmentation of their natural habitat. On the other hand,

Fig. 10.5 Massive “cleaning activity” of epiphytes in downtown Paramaribo (Suriname)

several bromeliad species frequently show substantial increases in abundance in secondary forest (Barthlott et al. 2001; Hietz et al. 2006; Larrea and Werner 2010).

Werner et al. (2011) offered an explanation for the diverging results of individual studies by suggesting a link between local climate and the effect of disturbance. They noted that the impact on epiphytes by isolating a tree is most pronounced in regions with moderately moist and seasonal forests. There, the diminution or loss of the vertical microclimatic gradient renders trees inhospitable for many epiphytes while in both aseasonally wet and distinctly dry regions growth conditions for epiphytes remain sufficiently wet or, alternatively, never were wet in the first place. Hence, there is hardly any decrease in species numbers. The available studies more or less agree with the expectation of a hump-shaped relationship of the degree of impoverishment and local moisture availability (Werner et al. 2011). A major complication when comparing these studies is the factor time. Largely ignorant of the long-term dynamics of both pristine and human-modified systems, discrepancies may result from comparing different stages during adjustment from primary forest conditions to a new steady state. A number of studies indicate that apart from immediate reductions further decreases in individual and species numbers are likely to occur, at least during the first years after a disturbance (“extinction debt,” Kuussaari et al. 2009). For example, Zotz (2005) studied the population growth rate (λ) of the bromeliad, *Vriesea sanguinolenta*, in a population growing on pasture trees in lowland Panama: λ was below unity. This is in line with reduced growth rates and a gradual impoverishment of epiphyte assemblages on isolated trees at montane sites in Ecuador (Köster et al. 2009; Werner 2011). Whether these

Fig. 10.6 Good hosts—bad hosts. (**a**) *Anacardium excelsum* is an example of a tree species in moist lowland forests that typically hosts a very rich epiphyte flora (BCI, Einzmann et al. 2015). Many tree ferns, particularly in montane forests like that in Fortuna, Panama, are also known to be good hosts (**b**, Sanger and Kirkpatrick 2014). Other tree taxa, e.g., those with flaking or very smooth bark like *Eucalyptus*, *Pinus*, or *Bursera* spp., are usually poor hosts. However, given enough diaspore pressure and very wet conditions, e.g., around the towns of Boquete and Santa Fé, Panama (c. 1100 m a.s.l.), individual *Eucalyptus* (**c**) or *Pinus* (**d**) trees may carry at least a few epiphytes. (Photographs: **a**, **d**: Helena Einzmann, **b**: Simon Pearce)

trends are primarily driven by a delayed response to microclimatic changes or by changes in the spatial structure of metapopulations and metacommunities is currently unresolved. These uncertainties ask for direct long-term observational and experimental studies, which should allow us to evaluate the long-term viability of epiphyte assemblages in human-modified landscapes.

Several studies have addressed the question of temporal dynamics after disturbance by comparing the vascular epiphyte communities in secondary forests of varying age (Benavides et al. 2006; Cascante-Marín et al. 2006; Woods and DeWalt 2013; Shoo et al. 2016). The study that covered the longest period of time, i.e., more than a century, was conducted in lowland Panama: Woods and DeWalt (2013) compared the epiphyte communities in secondary forests of different age (ranging from 35 to 115 years after land abandonment) with those of nearby old-growth forests. Quantifying epiphyte species richness, density, and composition, they were able to show that developing secondary forests are likely to recover old-growth epiphyte richness and composition eventually, but the process is exceedingly slow (Fig. 10.7): even after 115 years, species numbers and individual densities reached only about 75 % and 50 %, respectively, of those of a mature forest. Considering the geographic location of the plots, this finding cannot be attributed to large dispersal distances from potential source areas. The lack of large trees in older secondary forests cannot serve as explanation either—the highest number of large trees was actually found in 85-year-old stands. Considering the high dynamics found in

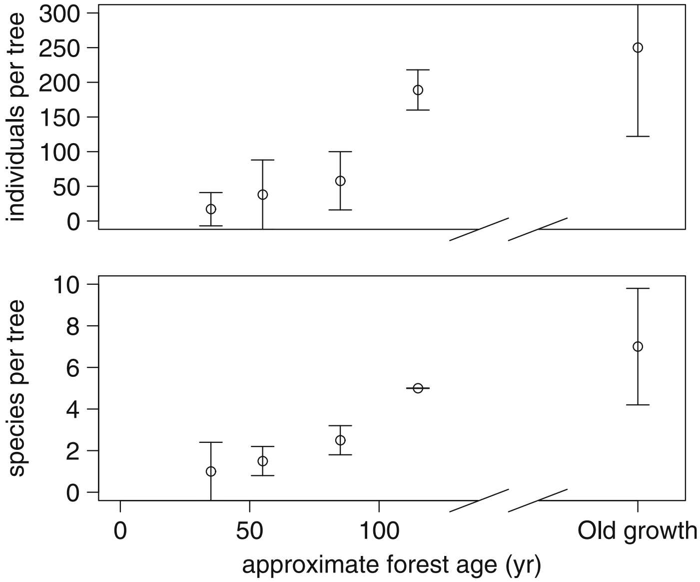

Fig. 10.7 Temporal changes in individual density and species richness of vascular epiphytes along a forest chronosequence in central Panama. Redrawn with permission after Woods and DeWalt (2013).

epiphyte communities in similar forest types in relative geographic proximity (Laube and Zotz 2006a), it is not entirely clear why recovery should take that long. However, these figures are quite comparable to those of a meta-analysis of some 90 studies on the recovery of *epiphytic lichens* in planted or secondary forests in temperate, boreal, and Mediterranean regions (Spake et al. 2015): the results suggest that it takes about 180 years to reach 90 % of old-growth values.

The usual increase of epiphyte abundance and species richness with tree size and age (Fig. 9.1, Flores-Palacios and García-Franco 2006) highlights the importance of large, emergent tree individuals for epiphytes (Sect. 7.1). Unfortunately, large old trees currently experience a global decline (Lindenmayer et al. 2012), and some negative consequences on epiphytes of previous land-use changes, which caused a change in tree size structure, may have gone unnoticed. For example, Laurance et al. (2000) showed that forest fragmentation in central Amazonia has a disproportionately severe effect on large trees—without mentioning the consequences for epiphytes. This dependence on large trees also indicates that selective logging activities in otherwise undisturbed forests are likely to have a much larger impact on local epiphyte assemblages than the number of extracted stems suggests (Hundera et al. 2013). Since tree species differ in their suitability as hosts, the picture should be particularly dim if timber trees were good hosts. This is exactly what Obermüller et al. (2012) found in Brazil when comparing the epiphytes on three timber tree species with those on other randomly selected tree species of similar size. The average number of epiphyte species per tree was three times higher in the timber species.

10.2 Human Health Issues

Many epiphytic orchids are part of the traditional medicine in South Africa (Chinsamy et al. 2011) and Asia (particularly China), but also South America (Ramos et al. 2012). Treated diseases range from mild diarrhea to tuberculosis or hepatitis (Hossain 2011). At least in a few cases, research has identified active compounds and validated the effectiveness of such therapeutic applications (e.g., Wang et al. 2010; Ramos et al. 2012); in most cases, however, the usefulness remains obscure. *Peperomia* species have received the greatest share of attention in regard to medicinal use and are particularly well studied (Kato and Furlan 2007). Again, applications are diverse, e.g., they serve as fungicide, trypanocide, anti-inflammatory, or cancerostatic via antiangiogenic action. Medicinal use is also reported for some epiphytic ferns (e.g., *Microgramma squamulosa*, Suffredini et al. 1999), aroids (Acebey et al. 2010), or bromeliads (Hornung-Leoni 2011), but overall the medicinal use of epiphytic plants is relatively limited. Collecting pressure is probably highest in Asia. The fact that several *Dendrobium* species have already gone locally extinct due to overexploitation has prompted Liu et al. (2014) to design a scheme for sustainable cultivation and protection for these species.

One of the classic studies on epiphyte ecology (Pittendrigh 1948) was initiated to understand particular epidemiological features of malaria in Trinidad. Bromeliad phytotelmata had been identified as frequent hosts of mosquito larvae that as adults act as vectors of malaria or dengue, such as *Anopheles* sp. or *Aedes aegyptii*. Continued public health concerns about phytotelmata have motivated a number of subsequent studies with bromeliads (e.g., Mocellin et al. 2009), but also with other taxa, e.g., *Collospermum hastatum* in the Asteliaceae (Derraik 2005). Although phytotelmata do indeed frequently host mosquito larvae, several studies in urban environments (e.g., Mocellin et al. 2009) have shown that the frequency of larvae in man-made containers is generally much higher. These authors conclude that pest control should thus focus on such containers and not on phytotelmata. Lopez et al. (2011) offer a convincing explanation for the relatively low occurrence of mosquitoes in phytotelmata. They demonstrate experimentally that the acidic conditions in these aquatic microcosm result in higher larval mortality. In conclusion, it is debatable whether health reasons can really justify the removal of epiphytic bromeliads near human settlements.

There are almost 30 published studies which have clearly established the usefulness of vascular epiphytes as bioindicators, which complements the long-standing use of nonvascular epiphytes, particularly lichens, for that purpose (Falla et al. 2000). Most studies focused on atmospheric *Tillandsia* species, but a few used ferns such as *Asplenium nidus* (Vtorova and Sergeeva 1999). The potentially harmful substances to human health that were tested range from heavy metals (Rodriguez et al. 2011) and hydrocarbons (Brighigna et al. 2002) to radionuclides (Somashekarappa et al. 1996). More recent studies also investigated the usefulness of epiphytic *Tillandsia velutina* to monitor and remove *indoor* atmospheric pollutants such as formaldehyde (Li et al. 2015). Although the results look generally promising, it remains to be shown whether the application of vascular epiphytes as bioindicators at larger scales will be feasible.

10.3 Epiphytes as Ornamentals and Non-Timber Forest Products

A recent review by Hornung-Leoni (2011) lists 78 species of Bromeliaceae, many epiphytic, which are used in Latin American countries as ornamentals, as food, as source of fiber, or in ceremonial contexts (Fig. 10.8). In Bolivia, the plant families Araceae and Bromeliaceae provide numerous non-timber forest products. Uses are manifold and could be greatly increased through effective management (Acebey et al. 2010). In some regions of Mesoamerica, epiphytic bromeliads and orchids play a particularly prominent part in religious ceremonies (Fig. 10.8, del Carmen Méndez García and Mondragón 2012). However, little is known about how the associated harvest impacts populations of epiphytic plants (Elliott and Ticktin 2013).

At a global scale, the sale of epiphytic orchids, aroids, bromeliads, and ferns has grown into a multimillion dollar industry over the last decades. Among orchids, hybrids of the epiphytic genera *Phalaenopsis* and *Dendrobium* are particularly important. Taiwan alone, the world’s top orchid exporting country since 2005,

Fig. 10.8 Use of epiphytes in religious ceremonies in Mexico. Several species of epiphytic bromeliads and other plants, which are taken from the wild, are used to produce floral arches (**a**, **b**, "Arco floral", Haeckel 2008) or as decoration in churches (**c**). During festivities, large quantities of epiphytes (e.g., *Tillandsia* or *Huperzia* species) are also sold to the general public by street vendors (**d**) (Photographs: **a**, **b**: Thorsten Krömer, **c**, **d**: Demetria Mondragón)

exported orchids for 87 Million US$ in 2009. Such quantities were made possible by industrial style tissue culture. Tissue culture is also common in the production of bromeliads, but some large producers in the Netherlands, which is currently the world's leading country in bromeliad production, propagate plants also from seeds at an industrial scale (Fig. 10.9). Of course, many small nurseries all around the world have epiphytic plants in their assortments. Unfortunately, wild populations of orchids, bromeliads, and ferns still suffer from, mostly illegal, collections. For example, a study in the State of Veracruz, Mexico, concluded that the annual volume of illegal local trade of epiphytic orchids was comparable to the average

Fig. 10.9 Large-scale production of *Guzmania* hybrids in greenhouses in the Netherlands. These plants are grown from seeds (Photograph: Corn Bak BV, Assendelft, The Netherlands)

legal export of the entire country (Flores-Palacios and Valencia-Diaz 2007). Two research teams investigated whether the harvesting of naturally fallen epiphytes could be a viable and sustainable alternative for collections from the canopy (Toledo-Aceves et al. 2014; Mondragón and Ticktin 2011). The results of these studies are promising, but it remains to be shown that the legal and social issues with the implementation of this practice can be resolved (discussed in detail by Toledo-Aceves et al. 2014). Ideally, the harvest of this non-timber forest product could lead to the conservation of epiphytes in intact forests and provide a reliable, additional source of income for the local human population.

10.4 Invasiveness

Globally, invasive species pose a major threat to biodiversity (Fig. 10.1, Sala et al. 2000), but the invasiveness of epiphytes seems to be low. This statement may be surprising in view of the magnitude of international trade with epiphytic orchids, aroids, bromeliads, and ferns, which are sold in enormous quantities as ornamental plants—as just outlined above, and also considering the large number of private collectors of orchids and bromeliads, particularly of tropical and subtropical countries.

The Global Compendium of Weeds (http://hear.org/gcw/ accessed November 2015) lists more than 40 terrestrial orchids, but only a single epiphytic orchid, *Tolumnia variegata*, as "weed." The few published examples from other sources concern an invasive *Hylocereus* species in South Africa (Foxcroft et al. 2008), an invasive twig orchid in Mexican coffee plantations (García-González et al. 2013), or the occasional, escaped fern (Tejedor and McAlpin 2000). There is a somewhat more serious problem with (hemiepiphytic) *Ficus* species in parts of the USA (Fig. 10.10, Riefner 2016), and the Florida Department of Environmental Protection banned the planting of four species of this genus from Miami-Dade County on the grounds that they are invasive. Even on oceanic islands, which may be more vulnerable to terrestrial exotics than the mainland (Simberloff 1995), there is not a single alien epiphyte that plays the role of an aggressive invader. None of the scattered publications on escaped epiphytes on islands, e.g., *Aechmea fasciata* on the Bermudas, *Vriesea gladioliflora* in Hawaii (Anonymous 2010), or *Dendrobium crumenatum* in Puerto Rico (Ackerman 2007), indicate that these would negatively affect the local flora. A comprehensive study of the Hawaiian fern flora revealed that virtually all aliens are terrestrials or lithophytes (Creese et al. 2011), although recently a number of epiphyte species from diverse genera (e.g., *Cymbidium*, *Dendrobium*, *Polystachya*, *Vanda*) seem to become naturalized in increasing numbers (J. Ackerman, pers. comm.). Epiphytes as a group may be unsuccessful

Fig. 10.10 Cases of naturalized epiphytes and hemiepiphytes. (**a**) Epiphytic *Nephrolepis cordifolia* (an Australasian native) on a palm in Long Beach, California and (**b**) hemiepiphytic *Ficus microcarpa* (lower plant, original Australasian) and *Ficus rubiginosa* (upper plant, original Australia) on *Phoenix canariensis* in Encinitas, California (Photographs: Rick Riefner)

invaders of new habitats, because their physiology is mostly tuned to nutrient-poor habitats with generally slow growth and low competitive ability, which clearly differs from the typical invasive terrestrial (van Kleunen et al. 2010). Thus, even when a facultatively autogamous species like *Vriesea gladioliflora* escapes into a new geographic area such as O'ahu, competitive exclusion of local epiphytes is not very likely.

However, there are examples of negative effects *on* resident epiphyte by alien flora and fauna. Alien tree species may affect local populations of epiphytes, since host trees generally differ in their suitability for the establishment and growth of epiphytes (Laube and Zotz 2006b). Hence, an introduced tree species may, when abundant, drastically change local epiphyte communities. A case in point is *Psidium cattleianum*, a tree native to Brazil and adjacent tropical South America, which has invaded a number of Islands in the Pacific (Mudd 2004; Baider et al. 2012). In Hawaii's cloud forests, this species supports substantially fewer epiphytes than native *Metrosideros polymorpha*, probably due to its smooth and peeling bark (Mudd 2004). Likewise, much fewer epiphytes grow on the invasive exotic tree fern *Cyathea cooperi* than on native Hawaiian tree ferns (Medeiros et al. 1993). Reduced epiphyte cover, in turn, reduces the forest stand water retention capacity for precipitation by c. 60 % in this Hawaiian forest (Mudd 2004) and thus substantially affects ecosystem function. Introduced pathogens or herbivores may similarly harm epiphytic flora. The best documented case concerns the weevil *Metamasius callizona*, inadvertently introduced to the southern USA from Central America, which has disastrous effects on epiphytic bromeliad populations in its new range (Cooper et al. 2014).

10.5 Epiphyte Conservation in Times of Global Change

At present, epiphytic flora is already affected by all six drivers of biodiversity change identified at the onset of this chapter, but land-use change and climatic changes are by far the most important processes. A changing climate leaves species with three options: (1) they may remain stationary and evolve *in situ*, (2) they may track appropriate niches and migrate, or (3) they go extinct (Fig. 10.11a, Holt 1990). Evidence from Pleistocene glaciations suggests that plants and animals typically respond to climatic change at ecological timescales via migration (Overpeck et al. 1992). Hence, the likely synergism between climate change and habitat fragmentation is the most threatening aspect of the ongoing climate change (Fig. 10.11b, Lovejoy and Hannah 2005).

Epiphytes have been called "particularly" vulnerable to global climate change (Benzing 1998; Lugo and Scatena 1992). As a general statement, this is probably not correct (Zotz and Bader 2009), but in habitats such as tropical cloud forests, which are characterized by continuously high moisture input, epiphytes may indeed be more susceptible than other life forms to changes in precipitation or humidity patterns. There is even experimental evidence for this claim (Nadkarni and Solano 2002). However, since habitat destruction and alteration are much more imminent

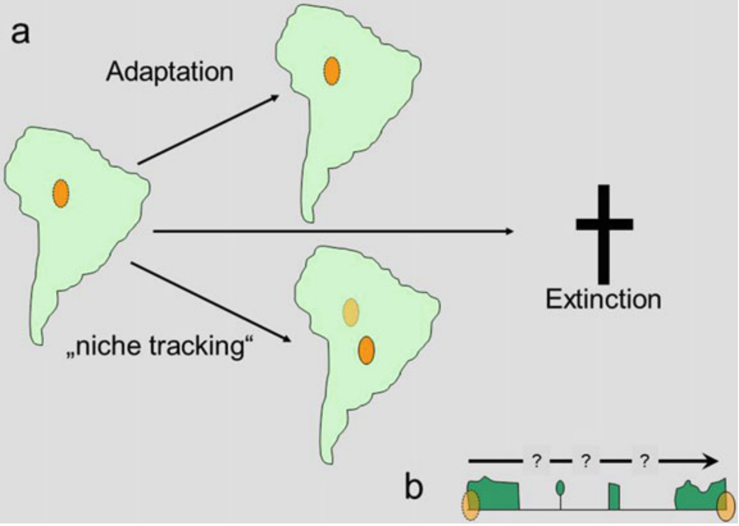

Fig. 10.11 Global change scenarios (after Holt 1990). In response to climate change, species may (1) evolve *in situ* (*ellipse with dotted line*), (2) migrate (*ellipse with solid line*), or (3) go extinct (**a**). Due to anthropogenic habitat fragmentation, option 2 (= migration) may no longer be possible (**b**).

threats for these systems, these also deserve the highest degree of imminent attention by science and society. Many epiphyte species can be easily cultivated in growing houses, in botanical gardens, or in private collections, even on artificial “supertrees” (Davey 2011) as in the Gardens by the Bay in Singapore. Thus, habitat destruction does not mean the immediate end of all locally occurring species, but the museal nature of such collections does not really make them an alternative to *in situ* conservation. *Ex situ* conservation in life collections or in seed banks (Vendrame et al. 2014) may be appropriate for transitional periods under particular circumstances, but does not offer a long-term perspective if appropriate habitats in the wild have been destroyed for good. As in biological conservation in general (Hambler and Canney 2012), we should protect functional systems, in which epiphytes can then thrive as one component of biological diversity, rather than focus on individual species. Such “functional systems” have to be of sufficient size, because edge effect alters microenvironmental conditions and also the dynamics of host trees (tree and branch falls) for hundreds of meters into forest fragments (Laurance and Bierregaard 1997).

Epiphytes are structurally dependent plants. Hence, it makes little sense to treat them in isolation from the biological systems in which they live. Apart from any *direct* effects of climate change, for example, altered precipitation patterns or temperature regimes on epiphytes, there are *indirect* ones, take the impacts of drought on host trees (Zhou et al. 2014; Nepstad et al. 2007) or an increase in forest dynamics due to a rise in liana densities (Phillips et al. 2005; Phillips et al. 2002). Thus, the extensive literature on global change effects on other components of, in particular, *tropical* biota is highly relevant for epiphytes—and is too extensive to be reviewed here. Rather, I would like to discuss some promising suggestions for more local solutions to some of the problems raised in this chapter. For example, there are a number of worked-out proposals for the sustainable cultivation of endangered medicinal plants (Liu et al. 2014) or of epiphytes used as ornamentals (Wolf and Konings 2001; Toledo-Aceves et al. 2014). Because of the potential conflicts between economic interests of local stakeholders and the protection of biodiversity, research that allows a rational evaluation of potential trade-offs and that highlights potential ways of "peaceful coexistence" is extremely valuable. I briefly describe three examples. Epiphytes are frequently removed in oil palm plantations because of a supposed negative impact on yield. However, Prescott et al. (2015) were able to show experimentally that epiphyte removal did not improve the production of fresh fruit bunches. Consequently, abolishing this practice makes sense economically for the plantation owner and at the same time avoids the destruction of epiphyte communities. Sporn et al. (2007) reached a similar conclusion for (nonvascular) epiphytes in Cacao plantations. Conversely, experimental removal of epiphytes in traditional coffee plantations in Mexico *did* lead to a substantial increase in crop production (Toledo-Aceves et al. 2013). The authors conducted a cost–benefit analysis of an alternative epiphyte management scheme, in which the negative impact of epiphytes on crop yields is more than balanced by the income generated by the long-term commercialization of fallen epiphytes as ornamental plants. Again, such an approach would reconcile economic and ecological interests.

Qualitative and quantitative changes in epiphyte communities have repercussions that go far beyond the epiphytes themselves. Preceding chapters (in particular Chaps. 8 and 9) have given ample evidence for the highly important and sometimes even indispensable role of epiphytes for the maintenance of a rich fauna in tree crowns (e.g., some of the anurans shown in Fig. 8.2). Similarly important is the role of epiphytes in ecosystem functions such as water and nutrient fluxes. Direct removal of epiphytes from tree crowns provides some quantitative measure of the consequences (e.g., Díaz et al. 2012), but it remains doubtful that such *localized* manipulations are really indicative of the full magnitude of the effects of a possible *regional* disappearance of epiphytes.

In a recent review, Wright (2010) describes in much detail possible scenarios for the future of tropical forests. Similar concerns were put forward for natural forests in the temperate zones (e.g., Armesto et al. 2009). By now, all ecosystems are affected by anthropogenic disturbance, because even the best protected and remote sites experience atmospheric and climatic changes. The prospects for many of these systems and their resident epiphytes are not too bright—but some of the described studies in this chapter give hope that there is a future for functional ecosystems with a large number of epiphyte species and associated flora and fauna on an increasingly human-dominated planet.

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Epilogue: The Epiphyte Syndrome

11

One of the most important questions that I wanted to address in this book was "what makes an epiphyte an epiphyte"? The length of this treatise demonstrates that there is no simple answer to this question. There is no single unique feature, neither anatomical, morphological, physiological, nor any other biological aspect that could be used to characterize vascular epiphytes and distinguish them unambiguously from soil-rooted flora. However, throughout this monograph I tried to identify traits that are particularly common or rare among epiphytes. These traits may be relevant for particular taxonomic groups with epiphytic members or for epiphytes in general. Some differences have been highlighted from the start of the scientific study of this plant group (e.g., small seeds, Schimper 1888), others are relatively new discoveries (e.g., longevity of gametophytes, Watkins and Cardelus 2012), some were expected and are easy to explain (e.g., a relatively high proportion of CAM species), others are less obvious and disputed (e.g., possible differences in genome size, Leitch et al. 2009; Chochai et al. 2012).

Considering the complex nature of the epiphytic habitat and the diverse taxonomic background of the participating flora, I would argue that the lack of a simple answer is not due to a lack of information, but a simple consequence of biology—there are many ways of being an epiphyte. Still, plants which typically occur as epiphytes are not just a random selection of the plant kingdom, and the accompanying table (Table 11.1) compiles all major features that are arguably "distinctive" for epiphytes and may be used to define something one could call the "epiphyte syndrome." Although none of the listed features is universal for all 28,000 known epiphytic taxa, this compilation should provide a useful reference for comparative studies. Go!

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Table 11.1 Traits which are particularly frequent or rare, respectively, among vascular epiphytes

Field	Trait/feature	Typical manifestation in epiphytes	Taxonomic group	Proposed explanation	Source	Contrasting evidence
A/M	Elaters	Common in epiphytic orchids, rare in terrestrials	Orchids	Dispersal	Hallé (1986)	
A/M	Gametophyte morphology	Strap-like or ribbon-like	Ferns and fern allies		Farrar et al. (2008)	
A/M	Dimorphy of fertile and sterile fronds	More common among epiphytes	Ferns		Watkins et al. (2016)	
A/M	Growth form	Sometimes pending	Orchids, cacti, ferns	Use of space	Diverse sources	
A/M	Inflorescence	Frequently pending, unusual for terrestrial herbs	Orchids	Use of space	Diverse sources	
A/M	Leaf succulence	More pronounced	Orchids	Overcoming intermittent water supply	Pridgeon (1993)	
A/M	Mesophyll idioblasts	Only in epiphytic taxa	"Throughout epiphytic orchids"	Increase water-storage capability, prevent cellular collapse during desiccation	Pridgeon (1993)	
A/M	Plant size	Generally smaller		Mechanical reasons	Nieder and Barthlott (2001), Chap. 4	
A/M	Roots with photosynthesis	Green roots with photosynthetic machinery	Orchids	Access to light	Many different sources	
A/M	Seeds	Generally small	Orchids, ferns	Need for vertical dispersal	Diverse sources	Rockwood (1985)
A/M	Stem succulence	Similar to ground-rooted taxa	Cacti		Diverse sources	
A/M	Tilosomes	Almost exclusively found in epiphytes	Orchids		Pridgeon et al. (1983)	Stern et al. (1993)
A/M	Impounding tank	Varied	Bromeliaceae, Asteliaceae	More continuous supply with water and nutrients	Benzing (2000)	

A/M	Bladder-like traps	Uniform and somewhat smaller traps	*Utricularia*		Reifenrath et al. (2006)	
A/M	Litter trapper	More common among epiphytes than among soil-rooted plants	Orchids, aroids, ferns	Improved access to nutrients	Zona and Christenhusz (2015)	
A/M	Velamen radicum	(Almost) universal in epiphytic orchids, also some other taxa (e.g., some *Anthurium*), but occasionally in terrestrial orchids and other taxa	Orchidaceae, Araceae		Arditti (1992)	
DEV	Germination	Asymbiotic germination much easier	*Cymbidium*		Arditti (1992)	
DEV	Germination	Faster in epiphytic species	Cactaceae		Paula and Ribeiro (2004)	
DEV	Germination and seedling development	Speed of development from seed to seedling much faster	*Cymbidium*		Chang et al. (2005)	
DEV	Vegetative growth	Extremely slow	Bromeliaceae, Orchidaceae	Trade-off growth stress tolerance	Schmidt and Zotz (2002, etc.)	
INT	Herbivory	Generally low	Bromeliaceae, Orchidaceae	Low nutritional value	Winkler et al. (2005)	
INT	Mycorrhiza	Lower levels of colonization	Ferns and lycophytes	Difficulty of establishment of mycorrhizal fungi in the canopy	Kessler et al. (2010)	
INT	Mycorrhiza	Distinct communities	Orchidaceae	Environmental constraints	Martos et al. (2012)	
PHYS	CAM	Overproportionally common compared to terrestrial plants	Orchidaceae, Bromeliaceae	Water economy	Silvera et al. (2009)	
PHYS	Cuticles	Extremely impermeable to water	Several		Helbsing et al. (2000)	

(continued)

Table 11.1 (continued)

Field	Trait/feature	Typical manifestation in epiphytes	Taxonomic group	Proposed explanation	Source	Contrasting evidence
PHYS	Genome size	Smaller	Orchidaceae	Selection for small guard cell sizes	Leitch et al. (2009)	Chochai et al. (2012)
PHYS	Osmotic potential	Less negative than in terrestrials in similarly dry habitats	Several	"All or nothing"	Zotz and Hietz (2001)	
PHYS	Roots	Separation of holdfast and absorptive function	Bromeliaceae, Araceae (nomadic vines)		Benzing (2000)	
PHYS	Stomatal behavior and light flecks	Slower photosynthetic response to lightflecks	Ferns, figs, orchids	Importance of water relations	Zhang et al. (2009a) and Zotz and Mikona (2003)	
PHYS	Water relations	Drought avoider, rarely poikilohydric	Ferns		Zhang et al. (2009b)	
POP	Gametophyte longevity	Long-lived, years to decades	Ferns		Watkins and Cardelus (2012)	
POP	Life history	Long-lived perennials, very rarely annuals	Several		Diverse sources	Chase (1986)

Traits are sorted by categories: *A/M* anatomy and morphology, *DEV* development, *PHYS* physiology, *POP* population biology, *INT* interactions with other organisms

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Glossary

Any glossary is subjective and incomplete. However, I hope that most unfamiliar terms the reader may encounter in the main text are included. I also encourage the reader to consult Moffett's (2000) excellent review of the terminology used by researchers interested in the forest canopy and its biota.

Abaxial	The surface of a leaf that faces away from the stem, usually the lower surface
Accidental epiphyte	A terrestrial species that occasionally can be found in tree crowns ($<5\,\%$ of all individuals). It may or may not reach maturity as epiphyte
Adaxial	The surface of a leaf that faces towards the stem, usually the upper surface
Aerenchyma	Spongy tissue with air channels and spaces
allelopathy	The phenomenon by which a plant produces secondary metabolites (allelochemicals) that negatively affect growth and survival of other co-occurring organisms
Allozyme	Variant form of an enzyme that is coded by different alleles of a single locus. Allozyme studies allow insights into the relatedness of species or individuals of a population
Amphistomatic	The condition of stomata being found on both leaf surfaces
Anemochory	Dispersal of diaspores by wind
Ant-house epiphyte	Epiphytic myrmecophyte with modified (chambered) stems or leaves (*myrmecodomatia*) that can house ant colonies
Apomorphic	Derived (↔ plesiomorphic)
Apoplast	The free diffusional space outside the cell membranes, comprised by all the cell walls of adjacent cells and all extracellular spaces in plant tissue.
Aquaporin	Integral protein of cell membranes, which selectively allows the passage of water molecules
Assemblage	→ "Ecological community"
Atmospheric/atmospheric epiphyte	A species entirely dependent on atmospheric inputs of moisture and nutrients, such as xerophytic *Tillandsia* species
Autogamy	Seed production possible by self-pollination ↔ outcrossing

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α, β, γ – diversity	Species diversity at the local scale (α) and the differences among habitats (β) determine total species diversity at the landscape scale (γ)
Bark epiphyte	Epiphyte that roots directly on tree bark without need for previous accumulation of organic material. Compare "canopy soil"
Bifacial leaf	The "typical" leaf, which has an upper and a lower surface that differ from each other
Bioindicator	An organism that is used to monitor the health of the environment
Bird nest fern	→ "nest epiphyte"
Canopy soil	Accumulation of dead organic material, plant roots and soil fauna, which can be substantial in both tropical and temperate forests
Carnivorous plant	Plant that captures and digests small animals, usually arthropods
Cenozoic	The current and most recent of the three geological eras of the Phanerozoic. It started 65 Mio years ago
Clade	A group of organisms that consists of a common ancestor and all descendents
Commensalistic	A type of symbiosis, in which on organism benefits from the other without negatively affecting it
Community	⟶ "Ecological community"
Conduplicate (leaves)	A lamina folded lengthwise
Constancy	The proportion of plots within a set of plots in which a given species occurs, which is equivalent to the probability of this species to be found in a randomly chosen plot
Crassulacean acid metabolism (CAM)	Photosynthetic pathway with nocturnal CO_2 uptake. Uptake during the day is also possible, which allows CAM plants to respond very flexibly to varying environmental conditions
Deciduous plant	Plant that regularly loses its leaves for part of the year ↔ evergreen plant
Dehydrins	Several proteins that plants produce during the stress response to drought and cold
Diaspore	A plant dispersal unit. This may be a single or several seeds or an entire fruit (seed plants), a spore (ferns), sometimes with additional tissues assisting in dispersal
Diazotroph	Organism that is capable of fixing atmospheric nitrogen
Ecological community	Local, potentially interacting collection of species, frequently used synonymously with "assemblage"
Endophyte	An endosymbiont that lives in plant tissue without causing apparent damage, frequently a bacterium or a fungus
Heliophile (plant)	A plant that needs large amounts of sunlight for establishment and growth
Epiphyll	A non-vascular organism (moss, liverwort, lichen, or alga) growing on a leaf surface
Epiphyte quotient	The percentage of epiphyte species in a local or regional flora
Evergreen plant	Plant with leaves throughout the year ↔ deciduous plant
Exodermis	A single-layered ring of cells between root cortex and velamen radicum. Most cells are dead and thick-walled, while living "passage cells" control the entry of water and nutrients into the cortex

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Extra-floral nectaries	Glands that secrete a sugar-rich liquid on any plant organ other than flowers (e.g., on stems, leaves, flower stalks, fruit)
Facultative epiphyte	A plant that is regularly but not exclusively found in tree crowns (5–95 % of all individuals)
Fractionation	A process that changes the relative abundances of different isotopes, caused by phase transitions, diffusional differences or enzymatic discrimination
Fruticose	Shrubby or shrublike
Gametangium	The organ of the gametophyte where the gametes (egg or sperm cells) are produced
Gametophyte	One of two free-living generations of ferns. This haploid, usually very small generation produces gametes. Compare Sporophyte
Gemma	The production of gemmae is a type of asexual reproduction. Gemmae consist of single or several cells, detach from the parent and develop into a new individual
Geotropism	Growth movement in response to gravity
Hemiepiphyte	Species that starts as true epiphyte but later establishes root contact with the soil. May eventually become free-standing (many hemiepiphytic *Ficus* spp.) or not (most hemiepiphytic *Clusia* spp.)
Hemiparasite	A parasitic plant that obtains water and mineral nutrients from the host plant, but is capable of photosynthesis
Heteroblasty	Sudden ontogenetic change in gross morphology from atmospheric to tank forms, particularly pronounced in many Tillandsioideae
Heterophylly	Simultaneous production of two distinct types of leaves
Holoepiphyte	A species which is exclusively found growing epiphytically. Compare facultative epiphyte and accidental epiphyte
Holoparasite	A parasitic plant that depends on a host for all resources (carbohydrates, water and mineral nutrients) → compare hemiparasite
Homoiohydry	The capacity to maintain relatively constant cell or tissue water contents (↔ poikilohydry)
Hypostomatic	The condition of stomata being confined to the lower leaf surface
Idioblast	An isolated plant cell that differs from neighboring tissues
Imbricate (leaves)	Overlapping at the base like tiles
Iteroparity	An iteroparous species has several reproductive cycles during its lifetime ↔ semelparity
Johansson zones (jzs)	A stratification scheme originally proposed for epiphyte assemblages on large trees. Typically, five zones are distinguished. These are not based on absolute height, but rather on the principal structures of the host tree (lower and upper portion of the trunk, central, middle and outer portion of the crown)
Mesophyte	A plant that shows no traits that are typical for very dry or very wet environments
Myrmecochory	Dispersal of diaspores by ants
Myrmecophyte	A plant that lives in a mutualistic association with one or several colonies of ants
Mycorrhiza	Symbiotic association of the roots of a vascular plant and a fungus

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Neoteny	In a neotenous species the morphology of reproductive individuals resembles that of young individuals. This is brought about by slowed somatic development
Nest epiphyte	Epiphyte which forms a rosette that impounds litter and moisture, but does normally not form a water-tight tank as some bromeliads do. The name "bird nest fern" is often used for several *Asplenium* species with similar morphology
Net primary production	The synthesis of organic compounds from atmospheric CO_2 by autotrophs less their respiratory losses
Nomadic vine	Climbing plant which usually germinates terrestrially and later loses the lower (proximal) portion of its stem. Contact to earth-soil may be maintained via adventitious feeder roots. Proposed to replace the term "secondary hemiepiphyte"
Outcrossing	Production of seeds where eggs and pollen stem from at least two genetically distinct individuals ↔ autogamy
Paleozoic	The earliest of the three geological eras of the Phanerozoic, which lasted from c. 540–250 Mio years ago
Phanerophyte	A category in Raunkiaer's life form system. It is categorized by stems that are projected in the air, and resting buds that are more than 25 cm above the soil level. Trees are typical representatives
Phorophyte	Structural support of epiphytes, typically a tree. I agree with (Moffett 2000) that the term is unnecessary jargon and its use should be discontinued
Phyllosphere	The total above-ground portions of plants as habitat for microorganisms
Phyllotaxis	The arrangement of leaves on a plant stem
Phytotelmata	Natural, water-holding plant cavity
Platyclade	Flattened, photosynthetic shoot; common, e.g., in cacti
Pleistocene	The first epoch of the Quaternary Period, from c. 2.6–0.01 Mio years BP
Plesiomorphic	An ancestral trait, frequently in comparison to another, derived trait (↔ apomorphic trait)
Plicate (leaf)	A lamina folded as a fan
Poikilohydry	The capacity to tolerate dehydration to low cell or tissue water contents and to recover from it without physiological damage. (↔ homoiohydry)
Populations growth rate (λ)	The rate at which the number of individuals in a population increases in a given period of time (usually a year), expressed as the fraction of the initial population size
Pseudobulb	A cylindrical to spherical stem found in many orchids, assumed to fulfil multiple storage functions
Sclerenchyma	Plant tissue with lignified cell walls that provides structural support
Secondary hemiepiphyte	→ Nomadic vine
Semelparity	A semelparous species has a single reproductive episode during its lifetime death, and iteroparous ↔ iteroparity
Sporophyte	One of two free-living generations of ferns. This diploid generation, which produces spores, is usually recognized as the "fern plant". Compare gametophyte

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Strangler	A hemiepiphyte that produces an anastomosing root system that envelops the host tree, which sometimes dies
Succulence	The condition of having fleshy plant parts (leaves, stems, roots) as a means to survive times of drought
Tilosome	A fibrous outgrowth, which is found in the velamen radicum of some orchids. The position above the transfer cells of the exodermis suggests a function in the reduction of water loss
Unifacial leaf	A leaf that has only an encircling adaxial or abaxial epidermis
Velamen radicum	A spongy, usually multilayered rhizodermis of many aerial and some terrestrial roots, composed of dead cells, typical for epiphytic orchids
Zoochory	Dispersal of diaspores by animals

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